PALAEOBIOGEOGRAPHY, EXTINCTIONS AND EVOLUTIONARY TRENDS IN THE CUNONIACEAE

A SYNTHESIS OF THE FOSSIL RECORD

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Submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy

University of Tasmania
November, 1999

Declaration

This thesis contains no material which has been accepted for the award of any other higher degree or graduate diploma in any tertiary institution and, to the best of my knowledge and belief, it contains no material previously published or written by any other person, except when due reference is made in the text of the thesis.

R. W. Barnes

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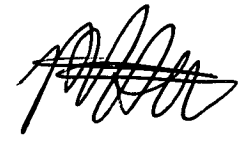

R. W. Barnes Date 13/3/00

I dedicate this thesis to Patches, for without her this work would never have been completed nor would I even be here. You will always be remembered and sadly missed.

'This is our last goodbye
I hate to feel the love between us die
But it's over
Just hear this and then I'll go you gave me more to live
for, more than you'll ever know.
This is our last embrace, must I dream and always see your face
Why can't we overcome this wall
Baby, maybe it's just because I didn't know you at all.'

Last Goodbye, Jeff Buckley (1966-1997)

Abstract

The fossil record of the flowering plant family Cunoniaceae is comprehensively examined and reviewed using detailed studies of the morphology of extant Cunoniaceae with new macrofossil species described from Australian Cainozoic sediments. Eleven of the 26 extant Cunoniaceae genera are represented in the macrofossil record and include leaves and leaf fragments, foliar cuticle and reproductive structures. These occur almost exclusively in Australian fossil deposits and range from Late Paleocene to Quaternary in age. Cunoniaceae fossil pollen is widely documented across the Southern Hemisphere but is less informative due to the low taxonomic resolution of its identification.

Leaf and infructescence macrofossils from five Cainozoic deposits in south-eastern Australia are indistinguishable from the extant species *Callicoma serratifolia* which is now restricted to eastern Australia. The first macrofossil of *Codia, C. australiensis*, is described from Western Australia, and has affinities with the juvenile foliage of at least one extant *Codia* species which is now endemic to New Caledonia.

Two new fossil species of *Ceratopetalum* are described from fruits, *C. westermannii* (late Early-Late Miocene) and *C. maslinensis* (Middle Eocene) and the identification of two others previously described, *C. priscum* (Middle Miocene) and *C. wilkinsonii* (Late Eocene-Early Oligocene), is supported.

Fossil *Eucryphia* capsules are described for the first time, *E. reticulata* (Early Oligocene) and *E.* sp. 'LRR1' (Early Oligocene), in addition to new species based on leaf macrofossils, *E. leaensis* (entire margin, Early Oligocene) and *E. mucronata* (serrate margin, ?Latest Eocene-Early Oligocene). The previously identified *E. aberensis* has been located at the early Oligocene Little Rapid River, making this the first *Eucryphia* species to be located in more than a single deposit. This species has both serrate and entire margins. Early Pleistocene leaves from Tasmania are conspecific with the two extant species, *E. lucida* and *E. milliganii* ssp. *milliganii*. The identification of *E. falcata* (Late Paleocene; Lake Bungarby) is supported.

Macrofossils and the fossil pollen record show that some genera had a different or more widespread distribution in Australia during the Cainozoic, with two genera (*Weinmannia* and *Codia*) having become extinct from the continent. A reduction in vegetation disturbance regimes (e.g. volcanism, uplifting, landslips) or changes in climate, including increasing cold, frost, dryness, seasonality, or some combination of

these, may be implicated in these generic extinctions, although the cause of others remains unidentified.

Many extant genera (*Schizomeria, Vesselowskya, Callicoma, Ceratopetalum, Acsmithia, Codia*) had evolved by the Early Oligocene or earlier (*Eucryphia*, Late Paleocene; *Weinmannia*, ?latest Eocene-Early Oligocene), perhaps with generic diversification more or less complete by the Early Cainozoic. A late Cretaceous origin of the family is possible, and may account for its widespread distribution on nearly all Southern Hemisphere landmasses, although long-distance dispersal events are required to explain some geographic disjunctions.

Foliar evolution has occurred at different rates within the Cunoniaceae. Within *Eucryphia* there has been an evolutionary trend towards simple leaves with entire margins and well developed peltiform cuticular extensions. These evolutionary trends and apparent adaptations are consistent with those proposed to have occurred within other prominent Cainozoic Australian rainforest genera, including a reduction in leaf size and increased protection of stomata. In contrast, the leaf form in *Callicoma* has remained relatively unchanged since the Early Oligocene which may be due to its paedomorphic origin from an ancestor shared with its sister taxon *Codia.*

A reduction in the flower size of two genera (*Acsmithia* and *Schizomeria*) provides support to the hypothesis that within some Cunoniaceae there has been a shift from entomophily to partial or exclusive anemophily. Petally in one extant and two fossil species of *Ceratopetalum* shows that petally was once more widespread in the genus. Secondary loss of petals may have been in response to fruit specialisation or a change in pollinator vector. Infructescences of *Callicoma* indicate that the genus has not changed florally since the Early Oligocene.

Acknowledgments

• I would like to thank my supervisors Prof. Robert Hill and Dr Greg Jordan for their support of my project and advice and constructive criticisms of my thesis and papers.
• I am greatly indebted to Jason C. Bradford (Washington University) and Dr Helen Hopkins (Kew) for providing me with extant Cunoniaceae specimens, words of encouragement and fruitful discussions on the complexities that are the Cunoniaceae.
• Dr Andrew Rozefelds (Tasmanian Herbarium) for access to extant specimens and helpful advice.
• Dr David Christophel (University of Adelaide), Dr Andrew Rowett (MESA, South Australia), Dr David Greenwood (Victorian University of Technology) and Dr Neville Alley (MESA, South Australia), Dr Robert Jones (Australian National Museum, Sydney) and Dr Imogen Poole (Leeds University) for fossil specimens, descriptions and information about site stratigraphy.
• Hans Westermann and Keith Holmes for fossil *Ceratopetalum* specimens.
• Dr Anita Cholewa (University of Minnesota), Dr Paul Forster (Queensland Herbarium), Dr Andrew Ford, Dr Bernie Hyland and Dr Elsa Zardini (Missouri Botanical Gardens) for specimens of Cunoniaceae.
• Deborah Edwards (Australian National Botanic Gardens), Annette Warner (Royal Melbourne Botanic Gardens), Carlos Lehnebach (Universidad Austral de Chile, Valdivia), Peter Goldblatt and Rachel Saunders (Silverhill Seeds, South Africa), Mark Fountain (Royal Tasmanian Botanic Gardens), Kylie Freebody (Eacham Shire Council, Queensland), Brett O'Donnell (Terania Nursery) and John Wrigley for plant material.
• Dr Mike Macphail and his technical assistant for pollen data and deposit ages.
• Gaye Johnson for administrative assistance and Ian Cummings and Tracey Jackson for glasshouse support.
• Dr David Steele for assistance with scanning electron microscopy.
• My friends through this process Colin McCoull, Yvonne Vucica, Alex Mitchell, Di Sward, Jenny Sheridan, Katie Dutch, Tim Brodribb, Lisa Schimanski, Vicki Carrol, Gloria Methorst, Melissa Sharpe and David Ziegeler.
• I thank Marcus Rowell, Melissa Sharpe, and Jenny Sheridan for going into the wilds of South America in the name of science. May the hunt for Cunoniaceae continue!
• Jeff Buckley provided me with words and music of inspiration and depression.

• I especially thank my family for having to put up with me and my thesis for the past 4 years, and those many friends that have stood by me through this entire process. If nothing else it has been an experience in life.

Preface

The majority of this thesis has been or is in the process of being published in scientific journals in conjunction with Professor Robert Hill or Dr Greg Jordan, who were the direct supervisors of the project. All the publications and papers in press that have resulted from this study are contained in Appendix 1, with each publication generally forming a chapter of this thesis.

The fossil identifications, morphological data and evolutionary concepts contained within these publications and thesis are my own, with some fossil specimens, technical support and editing provided by the co-authors (R.S.H. and G.J.J.). Data generated from this study also significantly contributed to the morphological and floral review of the genus *Anodopetalum* with Dr Andrew C. Rozefelds (Tasmanian Herbarium), who is reviewing Cunoniaceae for the Flora of Australia. This collaboration was a side project to the thesis but was important for understanding the floral and leaf morphology of *Ceratopetalum, Anodopetalum, Schizomeria* and *Platylophus.* The publication cited as Barnes *et al.* (2000) in this thesis was research conducted for my Honours project, and while it is directly relevant to aspects of this study (i.e. *Eucryphia*), it should not be assessed for this thesis.

As part of this study, I contributed to a collaborative project on the phylogeny of the Cunoniaceae with Jason C. Bradford, a Ph.D. candidate at the Washington University, who is studying the modern phylogeny of the Cunoniaceae and, in particular, the genus *Weinmannia.* I provided the micro-morphological and anatomical data to the publication, and corrected the final morphological dataset. The phylogenetic concepts and hypotheses in the manuscript are generally those of J. C. Bradford, or both of ours in collaboration. The use of the cladograms in this thesis are with the permission of J. C. Bradford, and have been generated from molecular data (J.C.B.) and morphological data (J.C.B. and R.W.B.).

In all cases, unless stated otherwise, the data and concepts presented in this thesis are my own.

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Chapter 1. Introduction

The Cunoniaceae are a geographically and morphologically diverse group of woody dicotyledons that are represented on every continental land mass in the Southern Hemisphere except for Antarctica (Table 1.1; Fig. 1.1). The floral architecture and morphology (Engler 1928; Dickison 1975*a*, 1984; Bradford 1998), nodal anatomy (Dickison 1980*a*), vegetative morphology (Dickison 1975*b*; Rao and Dickison 1985*a*, *b*; Dickison and Rutishauser 1990), wood anatomy (Dadswell and Eckersley 1938; Ingle and Dadswell 1956; Dickison 1980*b*) and pollen morphology (Hideux and Ferguson 1976) of the family have all been extensively studied.

The aim of this work is to provide a comprehensive study of the macrofossil record of the Cunoniaceae. Prior to this work the fossil record of the family was poorly known and patchily documented. This study will be based on detailed studies and comparisons of the morphology of both extant and fossil Cunoniaceae specimens. The Cunoniaceae lend themselves very well to a palaeobotanical study as they are already known to occur in the fossil record, with many Australian and overseas Cainozoic fossil deposits containing at least one macrofossil taxon considered to represent the family (e.g. Pole 1992; Pole *et al.* 1993; Hill and Merrifield 1993; Carpenter and Pole 1995).

Macrofossils considered to be representative of the the family (Table 1.2) include leaves and leaf fragments (Carpenter and Buchanan 1993; Hill and Merrifield 1993), dispersed cuticle (Carpenter and Pole 1995), wood (Petriella 1972), flowers (Carpenter and Buchanan 1993), fruits (Holmes and Holmes 1992) and seeds (Pocknall 1980). These have predominantly been identified from Cainozoic sediments in Australia with relatively few records from New Zealand (Pole 1993*b*), South America (Petriella 1972), Antarctica (Czajkowski and Rosler 1986) and Europe (Unger 1866). Cunoniaceae fossil pollen have also been widely documented (e.g. Sluiter 1991; Colhoun 1980) but is less informative due to the low taxonomic resolution of its identification and will therefore not be the focus of this study. Leaf and reproductive structures will be specifically studied as these are generally more common in macroflora assemblages and tend to preserve more data upon which to base a reliable identification than wood and pollen.

This study investigates the value of the macrofossil record in reconstructing the palaeogeographic distribution of the genera within the family. Previous studies have

Table 1.1. Genera in the family Cunoniaceae

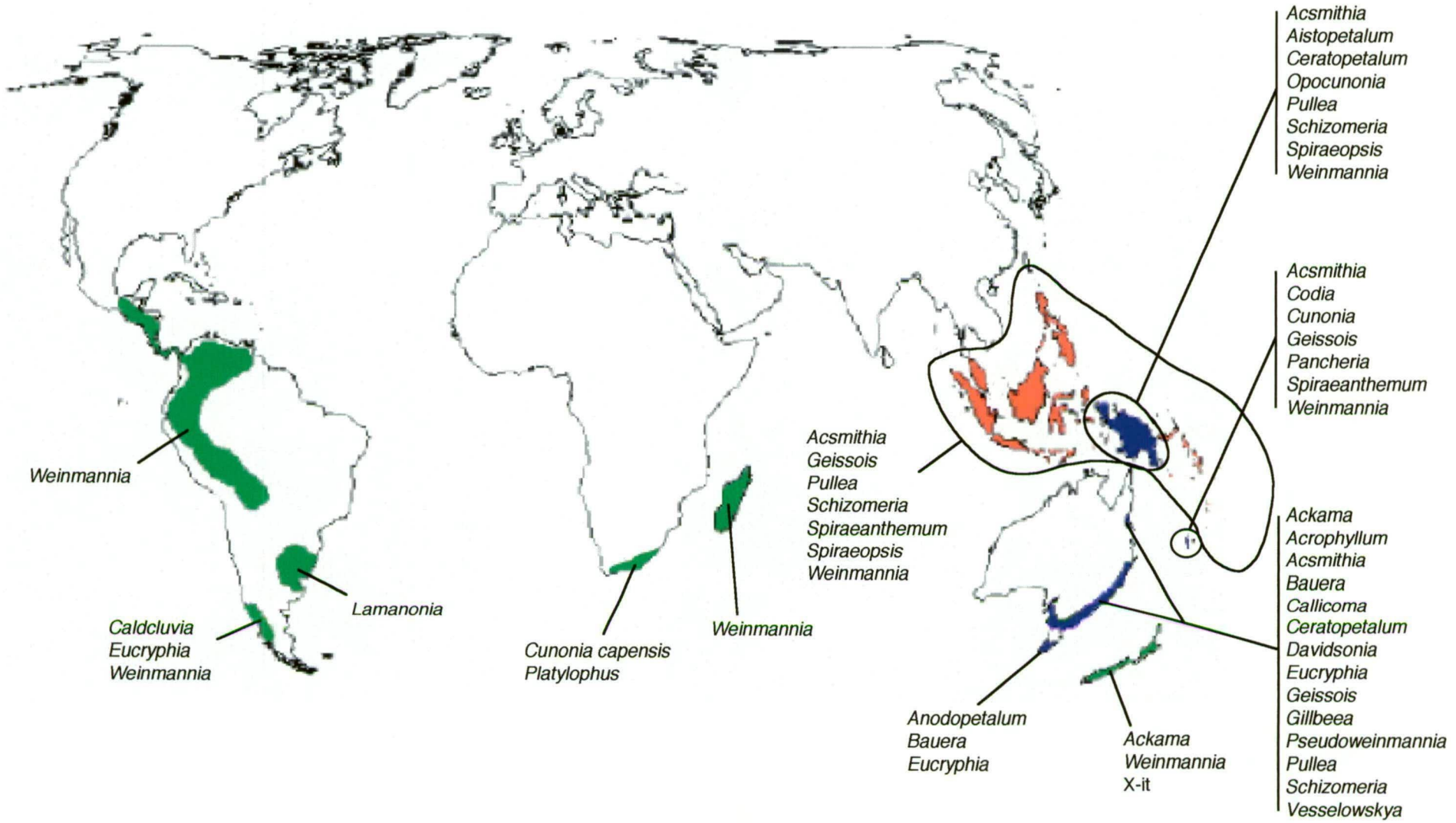
The number of species within each genus and their geographic distribution are also indicated. Recent taxonomic work has shown that *Pseudoweinmannia* contains 2 species (A.C. Rozefelds pers. com.) and *Gillbeea* is represented by 3 species (Rozefelds and Pellow in prep.).

Genus	No. of species	Geographic distribution
Ackama	3	New Zealand and eastern Australia
Acrophyllum	1	Eastern Australia
Acsmithia	ca. 14	New Caledonia, Fiji, Papua New Guinea, north-eastern Australia
Aistopetalum	2	Papua New Guinea
Anodopetalum	1	Tasmania
Bauera	4	South-eastern Australia and Tasmania
Caldcluvia	1	Chile
Callicoma	1	Eastern Australia
Ceratopetalum	8	Eastern and north-eastern Australia, Papua New Guinea
Codia	ca. 11	New Caledonia
Cunonia	24	New Caledonia (23 spp.) and southern Africa (1 sp.)
Davidsonia	3	Eastern and north-eastern Australia
Eucryphia	7	Eastern Australia, Tasmania and Chile
Geissois	ca. 18	Eastern Australia, New Caledonia, Fiji, Vanuatu and Solomon Islands
Gillbeea	3	North-eastern Australia, Papua New Guinea
Lamanonia	5	Southern Brazil, Paraguay and Argentina
Opocunonia	1	New Guinea
Pancheria	ca. 30	New Caledonia
Platylophus	1	southern Africa
Pseudoweinmannia	2	Eastern and north-eastern Australia
Pullea	3	North-eastern Australia, Fiji and eastern Malesia
Schizomeria	ca. 8	Eastern and north-eastern Australia, Papua New Guinea, Moluccas and the Solomon Islands
Spiraeanthemum	6	South Pacific Islands (e.g. Fiji and the Solomon Islands)
Spiraeopsis	6	Papua New Guinea, eastern Malesia and the Solomons
Vesselowskya	1	Eastern Australia
Weinmannia	ca. 150-160	Central and South America, Comores, Madagascar Mascarenes, Malesia, South Pacific and New Zealand

Fig. 1.1. World map showing the distribution of Cunoniaceae genera.

Regions shaded green have low generic diversity, those shaded red have moderate generic diversity while those areas shaded blue have a high degree of both generic diversity (>7 genera) and endemism. Many of these endemic genera are monotypic (see Table 1.1).

The small plant known as X-it from New Zealand has been assigned to Cunoniaceae on combined leaf and stem morphology and sequences of the chloroplast *rbc*L gene (see Garnock-Jones *et al.* 1996). Only a single plant has ever been recorded from the wild and has been propagated for conservation purposes.


Acsmithia
Aistopetalum
Ceratopetalum
Opocunonia
Pullea
Schizomeria
Spiraeopsis
Weinmannia
Acsmithia
Codia
Cunonia
Geissois
Pancheria
Spiraeanthemum
Weinmannia
Weinmannia
Acsmithia
Geissois
Pullea
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Spiraeanthemum
Spiraeopsis
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Acsmithia
Bauera
Callicoma
Ceratopetalum
Davidsonia
Eucryphia
Geissois
Gillbeea
Pseudoweinmannia
Pullea
Schizomeria
Vesselowskya
Lamanonia
Caldcluvia
Eucryphia
Weinmannia
Cunonia capensis
Platylophus
Weinmannia
Anodopetalum
Bauera
Eucryphia
Ackama
Weinmannia
X-it

Table 1.2. Macrofossils recorded in previous literature that were considered to represent the plant family Cunoniaceae

The macrofossils listed below are only those that were considered to represent the Cunoniaceae at the time that this thesis was completed. Some European records are not included as they have already been reassigned to other plant families in the past (e.g. see Mai 1995). Macrofossils may either represent an extinct or extant (denoted by an asterix) taxon. The taxonomic authorities for all taxa are listed in Appendix 2.

Genus or affinity	Species	Macrofossil type	Geological age	Site Locality	Source
Acsmithia	*grandiflora*	Flowers	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
Anodopetalum	*biglandulosum* *	Leaf with cuticle	Late Pleistocene	Melaleuca Inlet, Tasmania	Jordan *et al.* (1991)
Bauera	*rubioides* *	Leaves with cuticle	Late Pleistocene	Melaleuca Inlet, Tasmania	Jordan *et al.* (1991)
		Fruit			
Bauera	*rubioides* *	Leaves	Early to Middle Pleistocene	Regatta Point, Tasmania	Jordan *et al.* (1995)
Bauera	*rubioides* *	Leaves	Holocene	Moxon Saddle, Tasmania	Warren (1994)
Caldcluvia	*mirabilis*	Leaves	Tertiary	Seymour Island, Antarctica	Dusén (1908)
Caldcluvia	*mirabilis*	Leaves	Early Tertiary	King George Island, Antarctica	Czajkowski and Rosler (1986)
?*Caldcluvia*	*mirabilis*	Leaves	Early Tertiary	King George Island, Antarctica	Czajkowski and Rosler (1986)
Callicoma	*pannonica*	Leaf	Tertiary	Eperies, Austro-Hungary	Unger (1866)
Callicoma	*primaeva*	Leaf	Eocene	Vegetable Creek, Australia	Ettingshausen (1888)
Callicoma	*serratifolia* *	Leaf with cuticle	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
		Infructescence			
		Seeds with coat			
cf. *Callicoma*		Mineralised leaf	Middle Eocene-Oligocene	West Dale, Australia	Hill and Merriffield (1993)

Genus or affinity	Species	Macrofossil type	Geological age	Site Locality	Source
	sp. '*Callicoma*'	Leaf with cuticle	Late Oligocene	Berwick Quarry, Australia	Pole *et al.* (1993)
'Serrate-coarse' (*Callicoma*?)		Leaf impressions	Eocene	Eyre formation, Australia	Greenwood *et al.* (1990)
aff. *Callicoma*		Dispersed cuticle	Oligocene-Early Miocene	Morwell Formation, Australia	Blackburn (1985)
Ceratopetalum	*americanum*	Leaf	Tertiary	North America	Ettingshausen (1888)
Ceratopetalum	*bilinicum*	Leaf	Tertiary	Europe	Ettingshausen (1888)
Ceratopetalum	*gilesii*	Leaf	Late Eocene	Near Vegetable Creek, Australia	Ettingshausen (1888)
Ceratopetalum	*kaikoraiense*	Leaf impression	Pliocene (Late Miocene?)	Kaikorai Valley, New Zealand	Oliver (1936)
Ceratopetalum	*macdonaldi*	Leaf	Late Eocene	Near Vegetable Creek, Australia	Ettingshausen (1888)
Ceratopetalum	*pacificum*	Leaf impression	Later Pliocene	Ormond, New Zealand	Oliver (1928)
Ceratopetalum	*praearbutoides*	Leaf	Upper Tertiary	One Tree Point, Tasmania	Ettingshausen (1888)
Ceratopetalum	*primigenium*	Leaf	Tertiary	Ipswich Road, Australia	Ettingshausen (1894)
Ceratopetalum	*priscum*	Fruit	Middle Miocene	Chalk Mountain Formation, Australia	Holmes and Holmes (1992)
Ceratopetalum	*rivulare*	Leaf	Cretaceous	Grey River, New Zealand	Ettingshausen (1890)
Ceratopetalum	*wilkinsonii*	Fruit	Late Eocene-Early Oligocene	Vegetable Creek, Australia	Holmes and Holmes (1992)
Ceratopetalum	*woodii*	Leaves	Upper Tertiary	Geilston, Tasmania	Ettingshausen (1888)
Ceratopetalum		Fruit	Middle Eocene	Maslin Bay, South Australia	Christophel and Blackburn (1978)
Ceratopetalum	cf. *C. macdonaldii*	Leaves	Eocene-Recent	Melville Island, Australia	White (1974)

Genus or affinity	Species	Macrofossil type	Geological age	Site Locality	Source
Ceratopetalum	*clarkii*	Wood	Early Tertiary	Derby Deep Leads, Tasmania	Scott (circa 1937)
Ceratopetalum		Leaves	Early to Late Oligocene	Mt Bischoff, Tasmania	Johnston (1885)
Ceratopetalum	*radobojanum*	Leaf	?Tertiary	Radoboj, Croatia	Unger (1866)
Cunonia	*europea*	Leaf	?Tertiary	Radoboj, Croatia	Unger (1866)
Eucryphia	*aberensis*	Leaves	Late Eocene	Loch Aber, Tasmania	Hill (1991*a*)
Eucryphia	*falcata*	Leaves	Late Paleocene	Lake Bungarby, Australia	Hill (1991*a*)
Eucryphia	*gregorii*	Leaf	Tertiary	Pitfield, Australia	(Deane 1902*c*)
Eucryphia	*lucida* *	Leaves	Middle to Late Pleistocene	Pieman Dam, Tasmania	Colhoun (1980)
Eucryphia	*microstoma*	Leaf	Early Eocene	Regatta Point, Tasmania	Hill (1991*a*)
Eucryphia	aff. *milliganii*	Leaves	Early Pleistocene	Regatta Point, Tasmania	Hill (1991*a*)
Eucryphia	*lucida* *	Leaves	Middle Pleistocene	Regency Formation, Tasmania	Fitzsimons *et al.* (1990); Jordan (1992), Taylor (1993)
Eucryphia	*milliganii* *	Leaves	Middle Pleistocene	Regency Formation, Tasmania	Fitzsimons *et al.* (1990); Jordan (1992), Taylor (1993)
Eucryphia	sp.	Dispersed cuticle	Late Pleistocene	Melaleuca Inlet, Tasmania	Jordan *et al.* (1991)
Eucryphia	sp.	Dispersed cuticle	Early to Middle Pleistocene	Regatta Point, Tasmania	Jordan *et al.* (1995)
aff. *Geissois*		Dispersed cuticle	Early-Middle Miocene	Yallourn Formation, Australia	Blackburn (1985)
Phyllites	*yallournensis*	Leaves with cuticle	Oligocene-Middle Miocene	Morwell and Yallourn Formations, Australia	Cookson and Duigan (1950) Blackburn (1985)
Praegeissois	*weindorferi*	Wood	Miocene	Barrington, Tasmania	Scott (ca. 1937)

Genus or affinity	Species	Macrofossil type	Geological age	Site Locality	Source
Schizomeria	*tasmaniensis*	Flower	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
Spiraeanthemum/Acsmithia		Dispersed cuticle	Late Middle Eocene	Western Australia	Carpenter and Pole (1995)
Vesselowskya	aff. *rubifolia*	Leaf with cuticle	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
Weinmannia		Leaf impressions and seed cast	Tertiary?	Knocklofty, Tasmania	Milligan (1849)
Weinmannia	*bahiana*	?Leaflets	Pliocene	Bahia Province, Brazil	Krasser (1904)
Weinmannia	*brittoni*	?Leaflets	Pliocene	Potosi, eastern Bolivia	Berry (1917); Berry (1939)
Weinmannia	*potosina*	?Leaflets	Pliocene	Potosi, eastern Bolivia	Berry (1939)
Weinmannia	*racemosa* *	Seeds	Holocene	Lady Lake, New Zealand	Pocknall (1980)
?Weinmannia	*racemosa* *	Infructescence	Early Miocene	Manuherikia Group, New Zealand	Pole (1993*b*)
(?) *Weinmannia*	sp.	Leaves	Eocene?	Narracan, Australia	Chapman (1926)
Weinmannia - type		Wood fragments	Late Pleistocene	Mera, Ecuadorian Amazonia	Bush *et al.* (1990)
Weinmannia - type		Wood fragments	Late Pleistocene	San Juan Bosco, Ecuadorian Amazonia	Bush *et al.* (1990)
Weinmannioxylon	*pluriradiatum*	Petrified wood	Lower Tertiary (Paleocene)	Cerro Bororo, Chubut, Argentina	Petriella (1972)
Weinmannioxylon	*multiperforatum*	Petrified wood	Lower Tertiary (Paleocene)	Cerro Bororo, Chubut, Argentina	Petriella (1972)
Weinmanniaphyllum	*bernardii*	Leaf impressions	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
?Cunoniaceae	sp. 'small teeth'	Leaves with cuticle	Late Oligocene	Berwick Quarry, Australia	Pole *et al.* (1993)
?Cunoniaceae	sp. 'lanceolate'	Leaves with cuticle	Late Oligocene	Berwick Quarry, Australia	Pole *et al.* (1993)
?Cunoniaceae	Genus et species indet	Leaves with cuticle	Mid-Late Eocene	Hasties, Tasmania	Pole (1992)

recognised the biogeographic significance of the family (e.g. Bernardi 1963*b*), often noting the disjunct distribution of some genera (e.g. *Cunonia*, Hoogland *et al.* 1997), but none have included data provided by the fossil record. Regional or continental extinctions at the generic or family level will be described and hypotheses formulated to explain the possible cause or causes of such events. Cunoniaceae macrofossils may also provide a minimum age for the origin of the family, clades and genera if macrofossil identifications can be made to this taxonomic level.

The overall morphology of those genera with macrofossils of different stratigraphic ages will be examined in detail in an attempt to detect any evolutionary trend in form. Leaf macrofossils will be the principal focus of this part of the study as vegetative organs were much more likely to evolve significantly in response to climate change during the Cainozoic, especially in Australia, than other organs such as flowers, pollen and wood. This is because leaves, as principal sites of photosynthesis, are especially responsive to changes in temperature and water availability. Evolutionary trends in the morphology of reproductive structures will also be examined.

The detection of any trends in the evolution of leaf or floral form in the Cunoniaceae may firstly provide support for hypotheses generated from comparative morphology and phylogenetic studies of the family (e.g. Hufford and Dickison 1992), and include leaf reduction and petal loss. Secondly, any trends can act as an independent test of those evolutionary hypotheses generated from the study of macrofossils of other families, such as Podocarpaceae (*Acmopyle* and *Dacrycarpus*, Hill and Carpenter 1991), Nothofagaceae (*Nothofagus*, Hill 1983*a*, 1983*b*, 1991*b*, 1994) and Casuarinaceae (*Gymnostoma*, Hill 1994). These previous macrofossil studies have generally identified evolution in leaf form including leaf size, shape and phyllotaxy, patterns of stomatal distribution and the level of protection provided to the stomata (e.g. hairs, papillae, occurrence in pits). Explanations of morphological trends have invoked hypotheses of foliar evolution as an adaptation to a changing climate within Australia through the Cainozoic (e.g. Hill 1994). Similar evolutionary trends exhibited within the Cunoniaceae (e.g. leaf reduction, increased stomatal protection) may provide evidence in support of these hypotheses.

Thus, the general aims of this study were to:

i. examine the macrofossils previously assigned to the Cunoniaceae, and where-ever possible, to confirm, refine or reject their identification using detailed studies of the morphology of extant Cunoniaceae in the

context of phylogenetic studies;

ii. locate and describe previously unreported macrofossils of Cunoniaceae from selected Australian Cainozoic and Quaternary deposits;

iii. examine the palaeogeographic distribution of the Cunoniaceae based upon the accepted macrofossils, and to a lesser extent the fossil pollen, of the family, with a particular focus on detecting regional and/or continental extinctions;

iv. compare the morphology of extant and extinct species within the same genus in an attempt to elucidate any evolutionary trends that may be present, and to compare these trends to those shown in other families;

v. provide a minimum generic age for those genera represented in the macrofossil record;

vi. overlay these minimum ages onto a phylogeny of the family to provide a minimum age for the origin of clades at least, and for those genera not represented within the macrofossil record.

Thesis Outline

This thesis consists of seven chapters, including this introductory chapter which contains background information on the taxonomy, morphology and extant geographic distribution of the Cunoniaceae and a summary of the existing micro- and macrofossil record of the family. The second outlines the macrofossil specimens examined for this study, as well as providing background information on the fossiliferous deposits in which they occur and the methods used to sample extant taxa.

Chapters 3 to 5 constitute the bulk of this thesis and specifically review and discuss the macrofossil record of four Cunoniaceae genera (*Callicoma, Codia, Ceratopetalum* and *Eucryphia*). Each chapter firstly examines the extant vegetative and floral morphology of a specific genus or group of genera to provide data upon which to base macrofossil identifications. Macrofossils of each genus are then discussed in detail within each relevant chapter, with a brief discussion of their palaeogeographic and evolutionary significance. Chapter 6 reviews the macrofossil identification of several genera that are poorly known in the fossil record.

The data from the preceding four chapters is combined in Chapter 7 to provide a list of

accepted Cunoniaceae macrofossils. The significance and value of these in reconstructing the palaeogeographic distribution of the family and identifying regional expansions and extinctions are discussed. Evolutionary trends within genera and across the family are also identified and compared to those proposed for other families.

1.1 Taxonomy

1.1.1 Family Circumscription

The extant taxonomy of the Cunoniaceae has been extensively discussed (e.g. Bentham and Hooker 1862; Pampanini 1905; Baker 1921; Engler 1928; Perry 1949; Hutchinson 1967; Bernardi 1961, 1963*a*, 1964; Smith 1985; Hoogland 1960, 1979, 1981, 1988). Several genera have in part been recently taxonomically revised, such as *Weinmannia* (Bradford 1998; Hopkins 1998*a, b, c*; Hopkins and Florence 1998) and *Cunonia* (Hoogland *et al.* 1997). The taxonomy of the family is currently under review in several other projects, including Flora Malesiana (H. F. Hopkins pers. com.) and Flora of Australia (A. C. Rozefelds pers. com.).

The number of genera within the Cunoniaceae has varied between 23 and 28 as there has been an inconsistent acceptance of intra-familial taxonomic realignments and an ad hoc inclusion of genera that have previously been placed into their own monotypic families, including *Davidsonia* (Davidsoniaceae: Cronquist 1992; Harden 1990*b*), *Bauera* (Baueraceae: Hutchinson 1967; Everett 1990), and *Eucryphia* (Eucryphiaceae: Focke 1895, Bausch 1938; Thorne 1983; Harden 1990*c*).

The most controversial taxonomic realignment within the Cunoniaceae is the sinking of four previously recognised genera into *Caldcluvia* sensu lato by Hoogland (1979), who considered that *Caldcluvia* sensu stricto, *Ackama, Opocunonia* and *Spiraeopsis* 'are so similar in their flowers and fruits that their segregation in several genera as hitherto accepted is inconsistent with the level of generic distinctions elsewhere in the Cunoniaceae'. This realignment has received criticism based on fruit (Godley 1983) and seed (Webb and Simpson 1991) morphology. For this study, each of the 4 genera is recognised as a separate entity (Table 1.1), with all of these forming a monophyletic clade (see Bradford and Barnes manuscript submitted, Appendix 1).

Phylogenetic analyses incorporating molecular and/or morphological data support the inclusion of *Davidsonia, Bauera* and *Eucryphia* in the Cunoniaceae (Hufford and

Dickison 1992; APG 1998; Bradford and Barnes manuscript submitted, Appendix 1). Two genera previously included in the Cunoniaceae, *Aphanopetalum* (e.g. Hutchinson 1967; Clifford and Ludlow 1978; Harden 1990*a*) and *Brunellia*, have been excluded from this study. *Aphanopetalum* was shown by Hufford and Dickison (1992) to be nested within a clade containing *Bauera* and *Acrophyllum*. However, based on molecular (D. Soltis pers. com.; APG 1998), anatomical (Dickison *et al.* 1994) and palynological (Hideux and Ferguson 1976) evidence, the genus is now considered to be in *Saxifragcaeae* sensu lato. *Brunellia*, a South American endemic rainforest tree genus (Cuatrecasas 1970; Watson and Dallwitz 1992), has been suggested to be a genus in the family (e.g. Orozco 1997). However, the findings of Bradford and Barnes (manuscript submitted, Appendix 1) indicate that the genus is basal to the Cunoniaceae, and is more closely allied to the Australian endemic genus *Cephalotus* (Carlquist 1981).

Therefore, I consider the Cunoniaceae to be composed of 26 genera, and about 300 species (Table 1.1) with the common and widespread genus *Weinmannia* representing the majority of the estimated species total (ca. 150 spp., Bradford 1998; Hopkins 1998*a*). *Geissois, Pancheria* and *Cunonia* are also relatively speciose compared to other genera (see Table 1.1). The family occurs in the Oxalidales Heinze with the families Cephalotaceae, Elaeocarpaceae, Tremandraceae Connaraceae and Oxalidaceae (APG 1998). Brunelliaceae is also considered to be closely related to, but not included in, the Cunoniaceae (Bradford and Barnes manuscript submitted, Appendix 1).

1.1.2 Vegetative Morphology

The family has few distinguishing vegetative characters, although the presence of opposite, decussate leaves and interpetiolar stipules has been considered a characteristic feature of the family (Fig. 1.2.a-e). There are several notable exceptions to this, for example several genera have whorled (*Acsmithia*, Fig. 1.2.f) or spirally arranged leaves (*Davidsonia*, Floyd 1989) and stipules may occur in a lateral (e.g. Australian *Geissois, Lamanonia, Bauera*) or axillary (New Caledonian and Pacific *Geissois*) position relative to the leaves.

All genera have stipules, however these vary in their form, number and position relative to the leaves (e.g. Dickison and Rutishauser 1990; Rutishauser and Dickison 1990). For genera that have opposite and decussate phyllotaxy, the stipules are generally located in an interpetiolar position (Fig. 1.2.a-e), clasping the stem between

Figs 1.2.a-i. Stipule position and shape in selected Cunoniaceae genera.

Fig. 1.2.a. Interpetiolar stipules in *Ackama rosaefolia* from New Zealand are leafy in appearance and have a serrate margin (arrow). The imparipinnate leaves are formed by 5-9 leaflets, each with a serrate margin. Scale bar = 50 mm.

Fig. 1.2.b. Leafy interpetiolar stipules in the rare Australian species *Eucryphia jinksii*. Stipule margins are entire and pubescent. Scale bar = 10 mm.

Fig. 1.2.c. The large interpetiolar stipules in *Cunonia capensis* from South Africa have entire margins. This species has a disjunct distribution as all other *Cunonia* species occur within New Caledonia. The leaves are imparipinnate and develop within the enclosed stipules. Scale bar = 10 mm.

Fig. 1.2.d. Large interpetiolar stipules in *Weinmannia parviflora* from Fiji. Stipules either have serrate or entire margins in this genus. Scale bar = 10 mm.

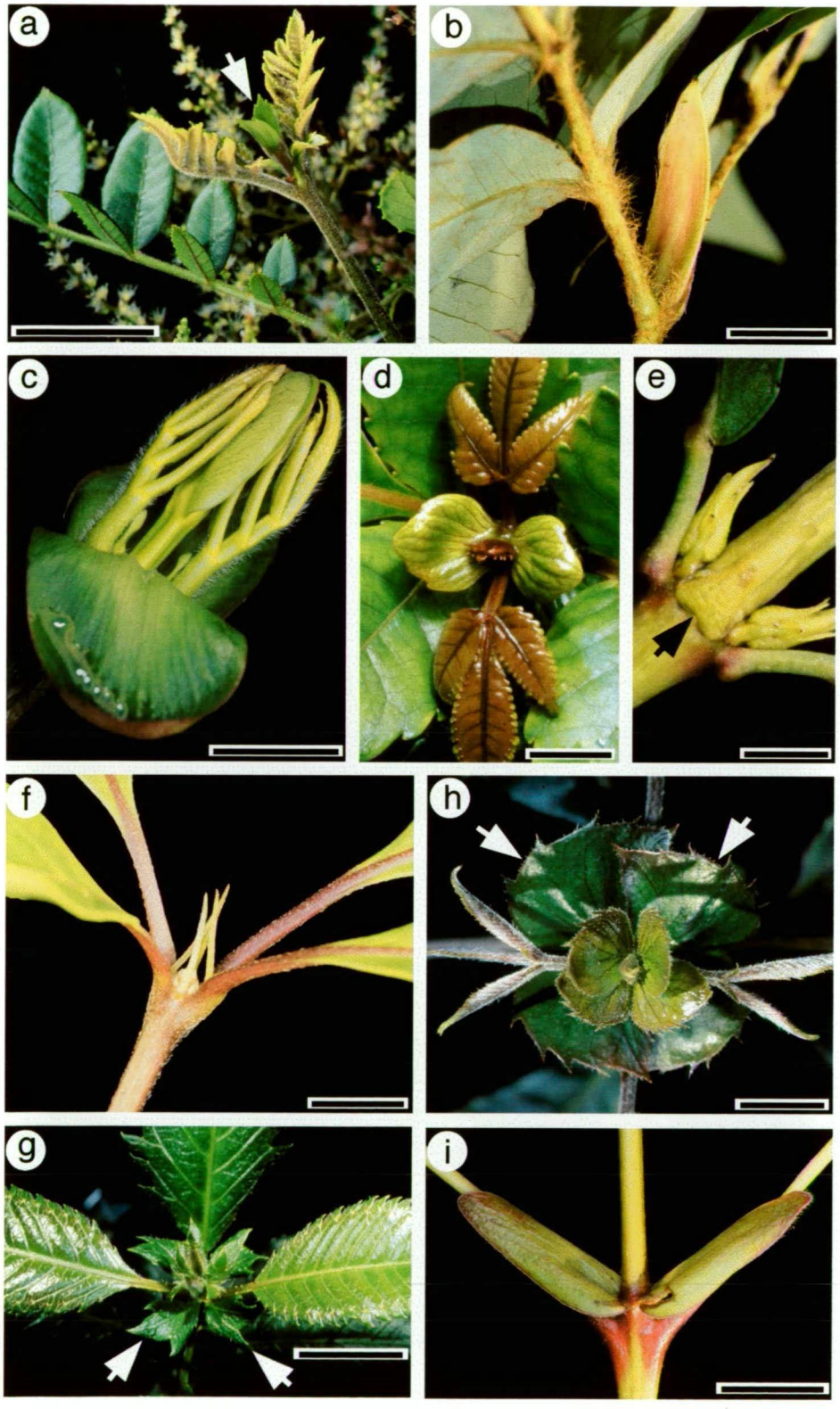
Fig. 1.2.e. Interpetiolar stipule in the Tasmanian endemic *Anodopetalum biglandulosum*. Arrow indicates the base of the stipule. Stipules are linear, scale-like and caducous. Scale bar = 5 mm.

Fig. 1.2.f. Interpetiolar stipules in *Acsmithia davidsonii* occur between the whorled simple leaves and are thin and linear. This species occurs in the rainforests of north-eastern Australia. Scale bar = 10 mm.

Fig. 1.2.g. Lateral stipules in the South American endemic *Caldcluvia paniculata*. The stipules are leaf-like and have a highly serrate margin. Scale bar = 10 mm.

Fig. 1.2.h. Large lateral stipules in *Geissois biagiana* from north-eastern Australia. Arrows indicate each overlapping stipule on one side of the stem. The stipules in mature trees tend to partially fuse at the base but remain distinct. Scale bar = 10 mm.

Fig. 1.2.i. Axillary stipules in a *Geissois* species from New Caledonia, which is a feature unique to these species within the Cunoniaceae. Scale bar = 10 mm.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the leaves and have formed from a single primordium (Rutishauser and Dickison 1990). The new leaves often develop extensively in the enclosed bud formed by these stipules (e.g. *Cunonia capensis*, Fig. 1.2.c). Stipules can be leaf-like and relatively large (e.g. Fig. 1.2.a-d) or small, scale-like and caducous (Fig. 1.2.e). Those genera that have whorled phyllotaxy, such as *Acsmithia* and *Acrophyllum*, have thin, often needle-like, interpetiolar stipules (e.g. *Acsmithia*, Fig. 1.2.f).

Lateral stipules occur in the South American endemic *Caldcluvia* s.s. (Fig. 1.2.g), Australian species of *Geissois* (Fig. 1.2.h), *Pseudoweinmannia, Lamanonia* and *Gillbeea* (see also Hoogland 1960, 1979; Dickison and Rutishauser 1990). Each stipule develops from a single primordium and either remains free at maturity or partially fuses to the adjacent stipule at maturity, as occurs in *Geissois biagiana* and *G. benthamii* from Australia (Dickison and Rutishauser 1990). New Caledonian and Pacific *Geissois* species have stipules in an axillary position (Fig. 1.2.i).

The wood anatomy of the Cunoniaceae in general, or specific genera, has been discussed by Dadswell and Eckersley (1938), Metcalfe and Chalk (1950), Ingle and Dadswell (1956), Dickison (1980*b*), Kennedy and Prakash (1981) and Rancusi *et al.* (1987).

1.1.3 Floral Morphology

Inflorescence architecture and floral morphology within the family is diverse (see Dickison 1975*b*). Most genera have paniculose (Fig. 1.3.a-b), cymose (Fig. 1.3.c) or racemose (Fig. 1.3.d) inflorescences formed by relatively small flowers. *Codia, Pancheria* and *Callicoma* (Fig. 1.3.e) have flowers clustered into spherical heads on a long peduncle. *Bauera* and *Eucryphia* species have solitary axillary flowers with large petals and numerous anthers (Fig. 1.3.f-g).

Individual flowers of all genera are actinomorphic (Harden 1990*a, b, c*) and generally bicarpellate, except for *Acsmithia* and *Spiraeanthemum* which have between 2 and 5 carpels (Hoogland 1979) and *Eucryphia* which can vary from 4 to 18 (Bausch 1938; Chapter 5 this study). Flowers may be petalous, apetalous or both within the same genus (e.g. *Ceratopetalum*).

Figs 1.3.a-g. Inflorescence architecture and floral morphology in selected Cunoniaceae genera.

Fig. 1.3.a. Paniculose inflorescence (top centre) and immature fruits (lower right) in *Ackama rosaefolia* from New Zealand. Individual flowers are small, petalous, diplostemonous and bicarpellate. Fruits at maturity are dry and ventrally dehiscent. Scale bar = 50 mm.

Fig. 1.3.b. A terminal paniculose inflorescence in *Acsmithia davidsonii* from north-eastern Australia. Flowers are very small, bisexual, apetalous and have 3 to 5 carpels. Scale bar = 50 mm.

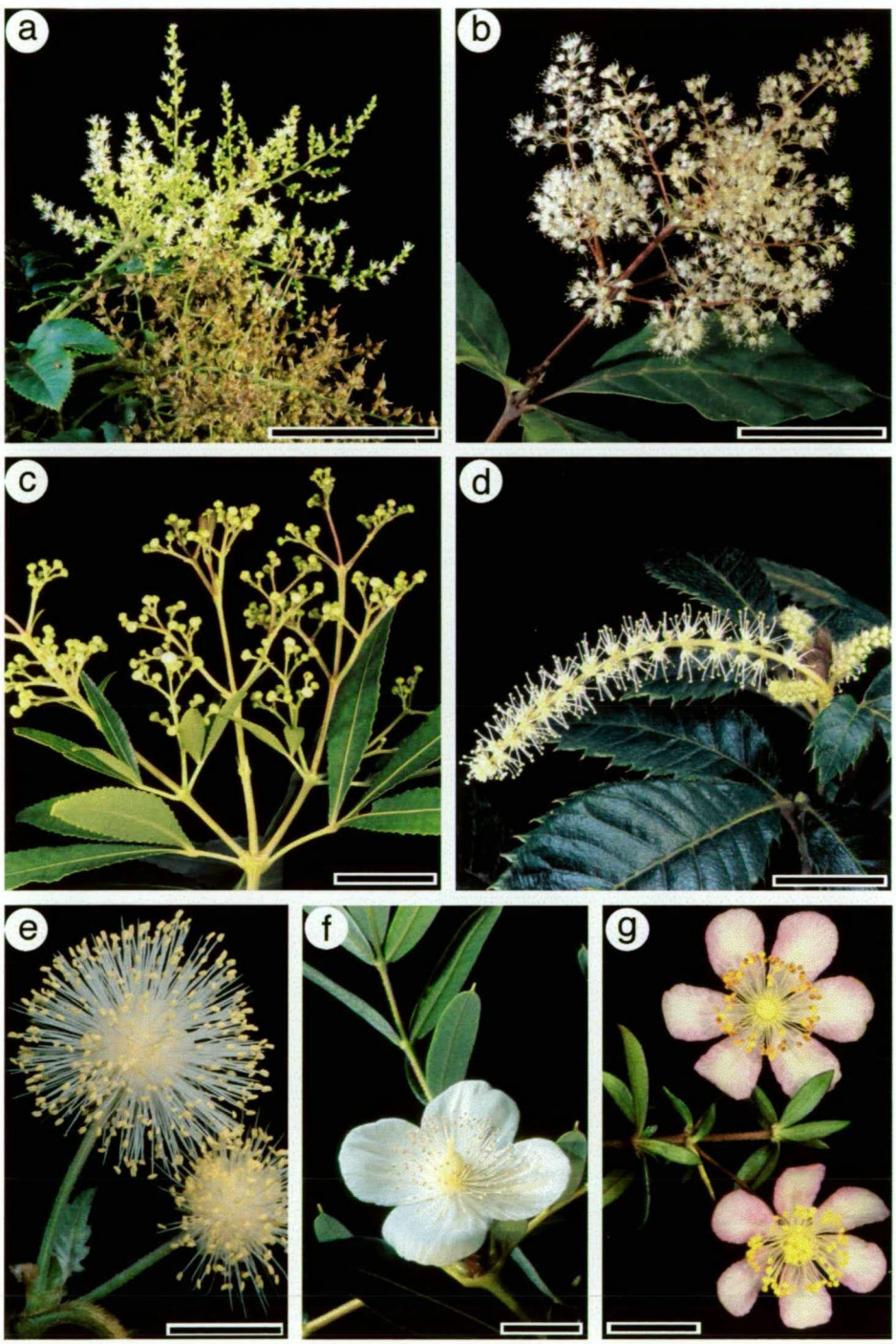
Fig. 1.3.c. Cymose inflorescence in *Ceratopetalum gummiferum* from eastern Australia. *Schizomeria* species also have a similar inflorescence architecture. Flowers in both genera have valvate calyx aestivation and are diplostemonous and bicarpellate. Bifid petals are present in all *Schizomeria* species but are restricted in *Ceratopetalum* to a single species, *C. gummiferum.* Scale bar = 20 mm.

Fig. 1.3.d. Racemose inflorescence in *Vesselowskya rubifolia.* The unisexual flowers are very small, with petals only occurring in the female flowers. Scale bar = 20 mm.

Fig. 1.3.e. Ball inflorescences in *Callicoma serratifolia* (black wattle) from eastern Australia. Scale bar = 10 mm.

Fig. 1.3.f. Solitary axillary flower in *Eucryphia moorei* (leatherwood) from south-eastern Australia. Flowers are polycarpelous and polystemenous. The petals are very large and showy. Scale bar = 10 mm.

Fig. 1.3.g. Solitary axillary flowers in *Bauera rubioides* from Tasmania and south-eastern Australia. Petals are large and showy compared to most other genera and range in colour from white through to deep pink. Scale bar = 10 mm.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1.2 Biogeography and Habitat

The family is represented on every Southern Hemisphere continent (excluding Antarctica) and numerous islands, including Madagascar, New Caledonia, New Zealand, Fiji and the Philippines (Fig. 1.1). *Weinmannia* is the most widespread genus (Fig. 1.1), extending into the cloud forests of Central America (Bernardi 1963*b*; Bradford 1998) and south-east Asia (Hopkins 1998*a*, *b*). Some genera are geographically disjunct, such as *Cunonia* which occurs in New Caledonia and southern Africa (Hoogland *et al.* 1997).

Most Cunoniaceae are generally canopy or sub-canopy trees (e.g. Hoogland 1960, 1979; Floyd 1989; Boland *et al.* 1985; Hopkins 1998*a*) that inhabit rainforest or wet forest habitats (Figs 1.4.a-d and 1.5.a-b). They often have a disturbance based ecology, and in some cases they are dependent on it for regeneration (e.g. *Weinmannia racemosa*, Stewart and Veblen 1982). Numerous *Weinmannia* species at least are pioneering shrubs or early successional plants as they tolerate the high light intensities created by canopy gaps and tree falls (Hopkins 1998*a*) although some can regenerate in the absence of disturbance (e.g. *Weinmannia trichosperma*, R.W. Barnes pers. obs.). Some of the species of *Eucryphia, Bauera, Callicoma* (Floyd 1989), *Anodopetalum, Ackama, Pullea, Caldcluvia, Ceratopetalum* and *Gillbeea* also have a similar disturbance based ecology.

Some genera have apparently become adapted to specific habitats, including *Codia* and *Pancheria* in New Caledonia, which are both extremely restricted in their distribution to ultra-mafic substrates dominated by maquis vegetation (Fig. 1.5.c). Most Cunoniaceae are poor soil specialists, including *Callicoma* and *Ceratopetalum* (Floyd 1989), although some are more prolific or restricted to basaltic soils or other soils of volcanic origin (e.g. *Schizomeria* and some *Weinmannia* species, Floyd 1989; Hopkins 1998*a*). The main centres of diversity and geographic distribution are discussed in detail below.

1.2.1 Australia

Generic diversity is highest within Australia where there are 15 genera; seven are endemic (Table 1.1) and four are monotypic (*Vesselowskya, Anodopetalum, Acrophyllum* and *Callicoma*). Centres of diversity are (i) Tasmania (ca. latitude 39-44° S), (ii) south-eastern and eastern Australia (latitude 25-37° S), and (iii) north-

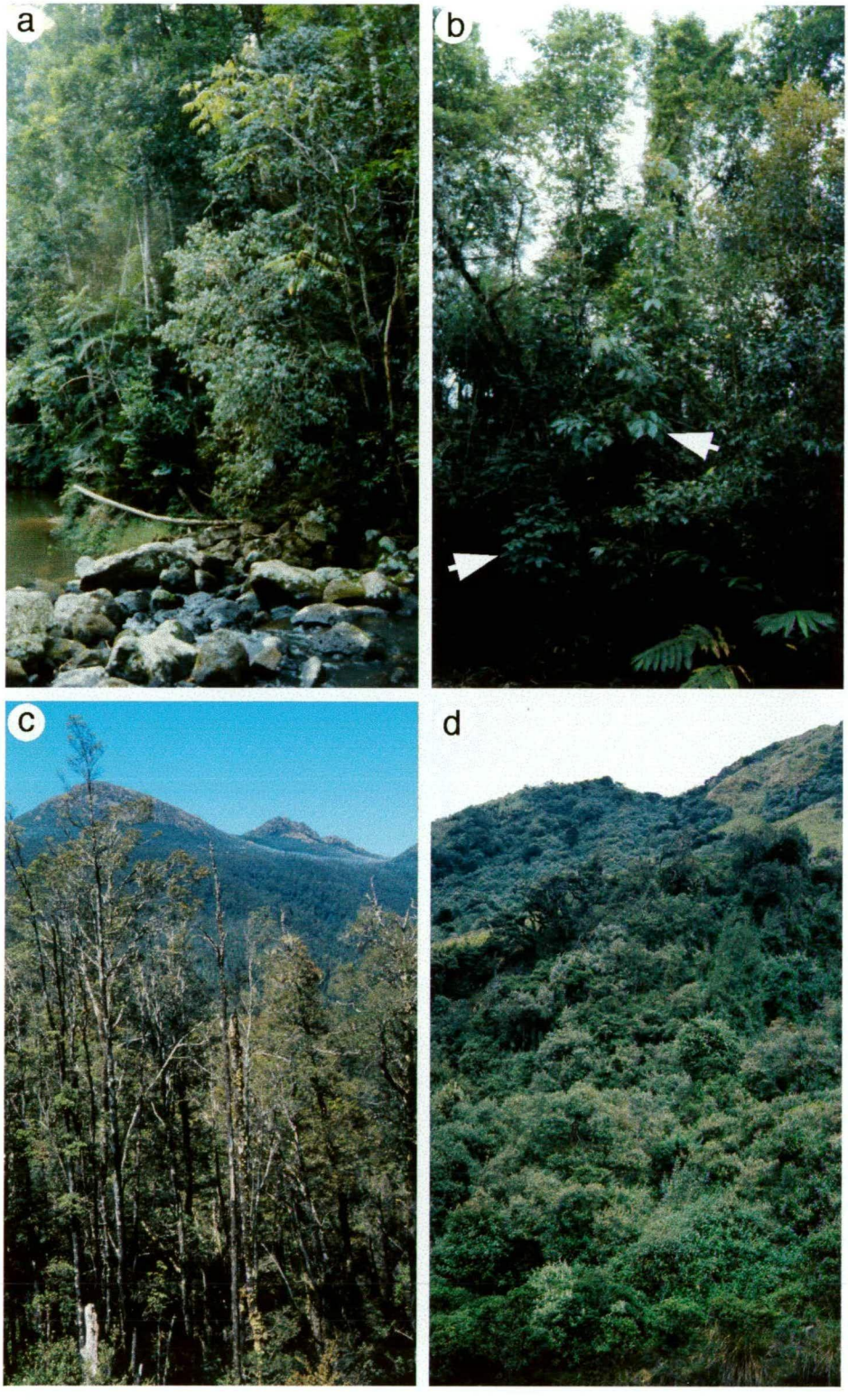
Figs 1.4.a-d. Forest habitat of Cunoniaceae genera.

Fig. 1.4.a. Upland well developed rainforest on the Atherton Tableland near Cairns in north-eastern Australia. This rainforest type in the region supports *Ceratopetalum* species, *Schizomeria ovata, Geissois biagiana* and *Gillbeea adenopetala.*

Fig. 1.4.b. Lowland tropical rainforest at sea level near the Daintree River in north-eastern Australia. A small shrub of *Gillbeea adenopetala* (left arrow) can be seen growing with a larger tree of *Geissois biagiana* (right arrow). *Gillbeea adenopetala* has large imparipinnate leaves and lateral stipules while *Geissois biagiana* can be recognised in the field by its large trifoliolate leaves and lateral stipules that partially fuse in adult trees. *Pullea stutzeri* and several *Ceratopetalum* species grow nearby as canopy trees, including the rare *C. macrophyllum.*

Fig. 1.4.c. Well developed cool temperate rainforest in Tasmania. Lowland callidendrous and thamnic rainforest supports tall trees of the Tasmanian endemic species *Anodopetalum biglandulosum* (horizontal) and *Eucryphia lucida* (leatherwood). The subspecies of *Eucryphia milliganii* replace *E. lucida* at higher altitude, but can also be found growing at lower elevations in everwet and frost prone habitats.

Fig. 1.4.d. Upland montane cloud forest in the central Ecuadorian Andes in South America. This type of forest is often dominated by several species of *Weinmannia.* Landslips are often common in these areas which generally enables the regeneration of *Weinmannia* species.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eastern Australia (latitude 14-20° S). Several genera are restricted to one of these regions, for example, *Anodopetalum* is endemic to Tasmania (Barnes and Rozefelds 2000, Appendix 1), *Vesselowskya* and *Callicoma* are restricted to the wet forests of eastern Australia (Francis 1981; Floyd 1989; Harden 1990*a*) and *Acsmithia* occurs in north-eastern Queensland (Hoogland 1979). *Geissois, Ackama, Ceratopetalum, Pseudoweinmannia* and *Schizomeria* occur in the latter two regions (Hoogland 1960; Williams *et al.* 1984; Floyd 1989; Stanley and Ross 1983; Harden 1990*a*) but are usually represented within each region by a different species, or a number of species. For example, *Ackama paniculosa* and *Geissois benthamii* occur in south-eastern and eastern Australia while *A. australiensis* and *G. biagiana* occur in north-eastern Australia (Hoogland 1960).

Bauera is an oddity in the Cunoniaceae as it has a wiry shrub habit. *Bauera rubioides* is widespread in Tasmania occurring in forest, scrub and open vegetation from sea level to the alpine zone, while this and other species (*B. rubioides, B. capitata* and *B. sessiliflora*) occur predominantly in dry coastal, riparian and montane environments on mainland southern and south-eastern Australia (Everett 1990). *Davidsonia* contains three species that grow as trees in small localised areas of rainforest in eastern and north-eastern Australia (Floyd 1989). Leaves are often covered in urticating hairs (Harden 1990*b*).

1.2.2 New Caledonia

Seven genera occur within New Caledonia, of which *Pancheria* and *Codia* are endemic (Schmid 1981). *Cunonia* is speciose in but not endemic to New Caledonia (ca. 23 spp.) as a single species, *Cunonia capensis*, occurs in South Africa (Hoogland *et al.* 1997; Palmer and Pitman 1972). *Cunonia* is morphologically similar to *Weinmannia* and has the autapomorph of acropetalous fruit dehiscence (Hoogland *et al.* 1997; Bradford 1998). Hopkins (1998*a*) suggests that *Weinmannia* is partly replaced in the New Caledonian vegetation by *Cunonia*, and probably accounts for its low species diversity (four endemic spp.). *Weinmannia* is restricted to humid montane forest habitats (Hopkins 1998*c*).

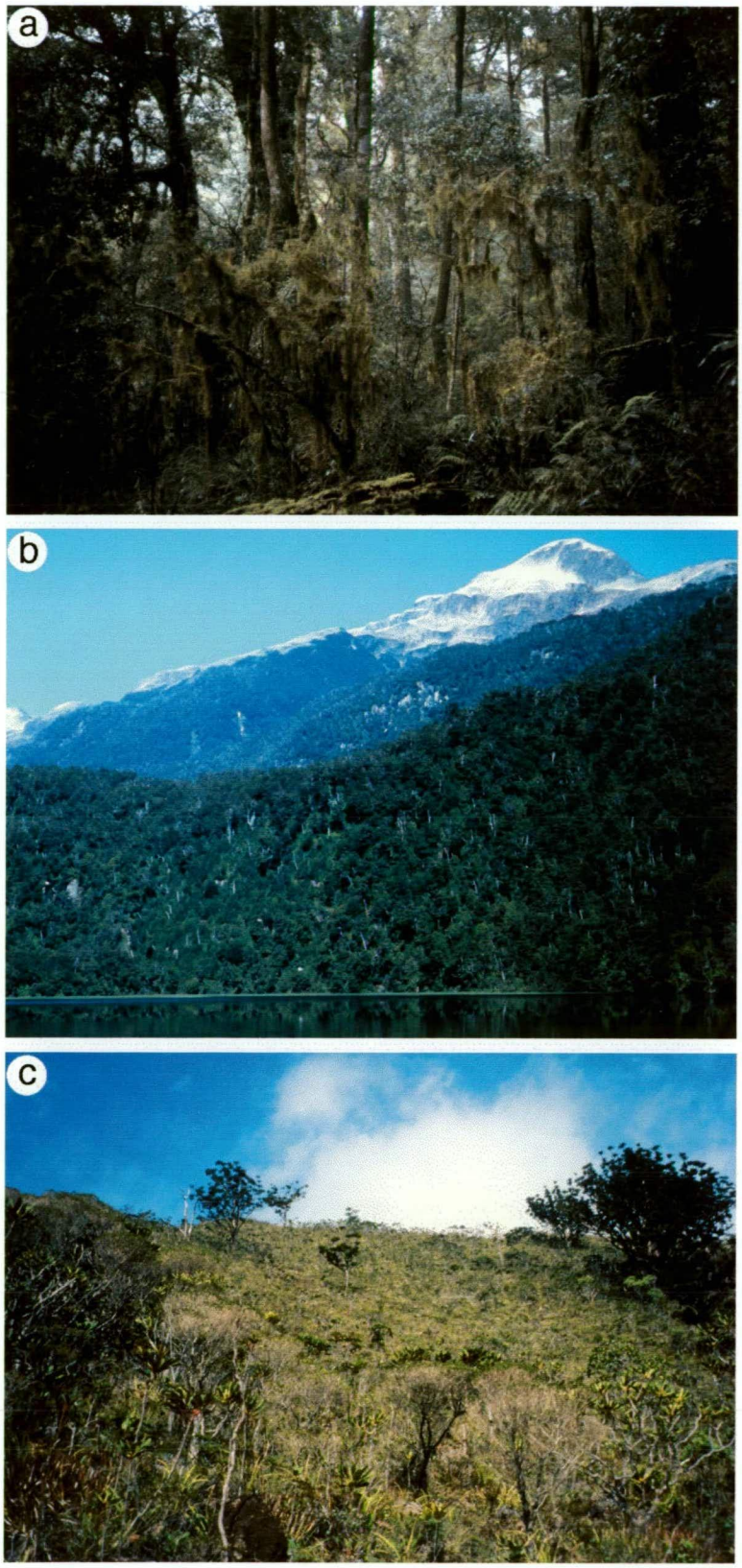
Species of several genera (e.g. *Pancheria, Codia* and *Cunonia*) occur in maquis vegetation (Fig. 1.5.c; Specht 1979) which is low open heath-like scrub with many sclerophyllous species. The soil is generally derived from ultra-mafic rock (Lowry 1998). The maquis is extremely fire prone, with at least one species of *Pancheria*

Figs 1.5.a-c. Habitats of Cunoniaceae genera.

Fig. 1.5.a. Tall, wet forest at Clyde Mountain in south-eastern Australia. *Callicoma serratifolia* occurs as a tree to tall shrub along the disturbed forest edge and open gullies while *Eucryphia moorei* occurs as a canopy and sub-canopy tree in the undisturbed forest.

Fig. 1.5.b. Cool temperate rainforest in southern Chile. These forests can experience snow at any time of the year and are very frost prone. The South American endemic species *Weinmannia trichosperma, Caldcluvia paniculata* and *Eucryphia cordifolia* all occur in these forests. Tree falls and canopy gaps are occasionally dominated by regrowth and seedlings of *W. trichosperma* and *C. paniculata. Eucryphia cordifolia* tends to occur in less disturbed forests.

Fig. 1.5.c. Maquis vegetation in New Caledonia. This vegetation is very open and heath-like in appearance and is very frequently burnt through human activities. Some *Codia, Cunonia* and *Pancheria* species occur in this vegetation type, especially on ultra-mafic substrates.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being adapted to this type of disturbance (Jaffré *et al.* 1998). *Geissois, Acsmithia* and *Spireaenthemum* species are trees to large shrubs and predominantly occur in rainforest or wet scrub (see Hoogland 1979, 1988), or rarely in maquis (e.g. *Geissois pruinosa*, Schmid 1981).

1.2.3 Papua New Guinea

Eight genera occur within Papua New Guinea, of which two are endemic (*Opocunonia* and *Aistopetalum*). The single species *Opocunonia nymanii* is a common and widespread tree of montane rainforest (Hoogland 1979). *Aistopetalum* is a genus of two species; *A. viticoides* occurs in primary forests in the west, north-west and north-east, while *A. multiflorum* is only known from the type location in central Papua New Guinea (Perry 1949; Hoogland 1960).

Spiraeopsis is represented by six species that grow as trees in higher altitude rainforest (Perry 1949; Hoogland 1979). Most of the vegetative and floral parts of the plant are covered in a variable indumentum of stellate and glandular hairs (Hoogland 1979). One species of *Ceratopetalum* (*C. succirubrum*) is widespread in forest habitats as well as occurring in north-eastern Australia (Hoogland 1960). The closely related genus *Schizomeria* is diverse with upwards of eight species occurring primarily in rainforest while *Pullea* is represented by two species that grow as trees in primary or secondary rainforest (Perry 1949). *Weinmannia* occurs as a tall tree to low shrub across several altitudinal ranges (500-3000 m a.s.l.) across the island (Perry 1949; Hopkins 1998*a*) while *Acsmithia* species grow as canopy trees in rainforest (Hoogland 1979).

1.2.4 New Zealand

Two species of *Weinmannia, W. racemosa* and *W. sylvicola*, and one species of *Ackama, A. rosaefolia* (Cockayne and Turner 1958; Wardle 1966; Hoogland 1979; Godley 1983; Bradford 1998; Hopkins 1998*c*) occur in New Zealand. The two allopatric species *W. racemosa* and *W. sylvicola* have different distributions and leaf forms; *W. racemosa* is abundant in the wet forests of both the South and North Island and has unifoliolate leaves, while *W. sylvicola* is restricted to the North Island and has predominantly trifoliolate leaves (Hopkins 1998*c*). *Ackama rosaefolia* is restricted to the North Island in forests and on forest margins and wet gullies (Hoogland 1979).

The small plant known as X-it from New Zealand has been assigned to Cunoniaceae on combined leaf and stem morphology and the chloroplast *rbc*L gene (see Garnock-Jones *et al.* 1996). It is only known from a single wild plant, which has been propagated for conservation purposes. Its affinities are most likely to be with *Weinmannia*, as suggested by Garnock-Jones *et al.* (1996), and is discussed further in Chapter 6.

1.2.5 Africa, Madagascar, the Mascarenes and Coromos Islands

Platylophus is a monotypic genus endemic to wet forest at the southern tip of Africa (Palmer and Pitman 1972; Seydack *et al.* 1995). The single species *Platylophus trifoliatus* grows along rivers and in the wetter parts of forest. It has tifoliolate leaves and cymose inflorescences and interestingly is reported by Palmer and Pitman (1972) to often occur as a stump with prolific, but crooked, side shoots, which is a growth habit also expressed in the genus *Anodopetalum* (see Barnes and Rozefelds 2000, Appendix 1). The fruits are tardily dehiscent and tend to form a swollen bladder at maturity and are eaten by birds (Palmer and Pitman 1972; Dickison 1984).

Cunonia capensis grows as a tree or shrub in moist forests in the Cape region and eastern Transvaal mountains (Palmer and Pitman 1972). The species is a prolific seed setter, with most seed dispersed by wind, and is generally fire resistant and capable of shading out other trees so that it dominates the vegetation (Palmer and Pitman 1972).

Madagascar contains a diverse array of *Weinmannia* species (ca. 40), most of which are endemic (Bradford 1998). They frequently occur in the middle to upper limits of forest (Bernardi 1963*b*; 1965; Bradford 1998). Several species are also distributed throughout the Mascarenes and Coromos Islands (Bernardi 1963*b*) but none occur on mainland Africa.

1.2.6 Malesia and the South Pacific Islands

Species of seven genera are dispersed throughout Malesia and the islands of the South Pacific region, with some species endemic to a single island (e.g. Fiji or Samoa). *Weinmannia* is the most widespread genus, occurring in the Mascarenes, Fiji, Samoa, Borneo, the Philippines and Lesser Sundra Islands (Hopkins 1998*a*, *b*, *c*; Hopkins and Florence 1998). It generally grows as a small tree to shrub in upland habitats that

are associated with natural disturbances, although some occur near sea level (Hopkins 1998*a*). It is often an early coloniser and has been able to disperse to many volcanic islands in the Pacific, presumably with the aid of its winged seeds (Hopkins 1998*a*).

Geissois extends into the New Hebrides and Fiji, from its predominantly Australian and New Caledonian strongholds (Smith 1952). *Acsmithia* occurs in eastern Malesia and Fiji, in addition to Papua New Guinea and north-eastern Australia (Hoogland 1979). Species of *Spireaenthemum* occur in Samoa, the Solomon Islands, and New Hebrides (Smith 1952; Hoogland 1979). A single species of *Pullea* is endemic to Fiji (Smith 1952). *Schizomeria* and *Spiraeopsis* species extend their range from Papua New Guinea onto some surrounding islands (e.g. Solomon Islands, Hoogland 1979).

1.2.7 South and Central America

Only four genera occur within South and Central America, of which two are endemic (*Lamanonia* and *Caldcluvia* s.s.). The region contains the highest number of species, mainly in the genus *Weinmannia* which is a common shrub to small tree in the cool, montane cloud forests of the Andes below an altitude of 3500 m (Schreve-Brinkman 1978; Rios 1986; Bradford 1998). It often dominates the vegetation on the western side of the Andes, especially in Colombia where the climate is more humid than that to the east (Bakker and Salomons 1989). Highest species diversity occurs in Ecuador (J. C. Bradford pers. com.), Colombia (van de Hammen 1981) and Peru with only a single species, *W. trichosperma*, occurring south of the Peruvian Andes where it occurs in the coastal mountains and Andes in Chile and Argentina (Rancusi *et al.* 1987). Numerous *Weinmannia* species also occur in Central America, including Panama, Costa Rica and Honduras (Bernardi 1963*b*).

Caldcluvia paniculata grows as a small tree in disturbed habitats and coastal vegetation between latitudes 30° 30' and 43° S in Chile and Argentina (Rancusi *et al.* 1987). Two *Eucryphia* species occur in Chile, including *E. cordifolia* that grows as a canopy tree on both the coastal mountains and Andes up to 700 m a.s.l. (Rancusi *et al.* 1987; Zegers 1995). *Eucryphia glutinosa* is a rare shrub that grows between 250 and 900 m a.s.l. in the foothills of the Chilean Andes (approximately 36° to 39° S) often around lakes and other water bodies, and is winter semi-deciduous (Rodriguez *et al.* 1983; Rancusi *et al.* 1987; Zegers and Garcia 1994).

Lamanonia grows in seasonally dry forests of Paraguay, north-eastern Argentina and

south-eastern Brazil (E. Zardini pers. com.). The genus has opposite, decussate trifoliolate leaves and unfused lateral stipules associated with each leaf pair. Its closest relative is *Geissois* in Australia.

1.3 Cunoniaceae Fossil Record

The Cunoniaceae fossil record can be divided into two categories, macrofossils and fossil pollen. Summaries of the relevant literature of both types of fossil are provided below as a background to this study.

1.3.1 Macrofossil Record

Cunoniaceae macrofossils remain poorly documented and understood compared to other families such as Proteaceae (e.g. Cookson and Duigan 1950; Hill and Christophel 1988; Carpenter and Jordan 1997; Vadala and Drinnan 1998; Jordan *et al.* 1998) and Nothofagaceae (e.g. Hill 1983*a*, 1983*b*, 1984*a*, 1991*b*). Historically, the assignment of a macrofossil to the Cunoniaceae has been based solely on a morphological similarity to an extant genus, which is more so for older leaf records (e.g. Milligan 1849; Ettingshausen 1888; Britton 1893; Chapman 1926). Recent macrofossil identification techniques have used a combination of leaf architecture and cuticular morphology to enable a more confident taxonomic assignment to a modern plant family or genus. This has been successful for macrofossils of Nothofagaceae (Hill 1984*a*, 1991*a*; Pole 1993*a*), Podocarpaceae (Hill 1989; Hill and Carpenter 1991), Araucariaceae (Bigwood and Hill 1985; Hill 1990), Proteaceae (Carpenter and Hill 1988; Carpenter 1994) and Lauraceae (Hill 1986; Pole 1996). In comparison, and with the exception of *Eucryphia* (Hill 1991*b*; Taylor and Hill 1996), little research has been conducted on the features of Cunoniaceae as a whole, or specific genera, to enable confident assignment of vegetative and reproductive macrofossils to this family.

Work by Ettingshausen (1888, 1890, 1894), in his contribution to understanding Tertiary macrofloras of Australia, yielded fossil leaf species of *Ceratopetalum* and one of *Callicoma*. Numerous macrofossils since have been assigned to, or proposed to have their affinities with, the Cunoniaceae.

Prior to this work the most comprehensive Cunoniaceae macrofossil study was

conducted by Carpenter and Buchanan (1993) who identified 5 species, representing 5 genera, from Early Oligocene sediments at Cethana in north-central Tasmania. Two of these genera were represented by flowers (*Schizomeria* and *Acsmithia*), two by foliage (*Vesselowskya* and *Weinmanniaphyllum*) whilst *Callicoma* was represented by both an infructescence and a single incomplete leaf macrofossil. All taxa are now extinct from Tasmania and, with the exceptions of *Vesselowskya* aff. *rubifolia* and *Callicoma serratifolia*, most likely represent extinct species (Carpenter and Buchanan 1993). Leaf macrofossils of *Eucryphia* have been extensively studied by Hill (1991*a*) and Taylor and Hill (1996).

Some macrofossils have been assigned to an extant genus, while others have only tentatively been suggested to have affinities with an extant genus (Table 1.2). For example, some macrofossils have been documented as having affinities to extant *Callicoma* and include an incomplete mineralised leaf (cf. *Callicoma*) from Middle Eocene-Oligocene sediments at West Dale in south-western Australia (Hill and Merrifield 1993), leaf compressions (?Cunoniaceae sp. *'Callicoma'*) from the Late Oligocene sediments at Berwick Quarry in Victoria (Pole *et al.* 1993), and leaf impressions ('Serrate-coarse' cf. *Callicoma*) from Miocene-Pliocene silcrete (Rowett 1997) at Stuart Creek in South Australia (Greenwood *et al.* 1990). In these cases, the fossils were not assigned to an extant or extinct species due to insufficient data to base a formal identification.

In a more broad identification, some macrofossils have been assigned to the family, or to a Cunoniaceae/Elaeocarpaceae complex as there has been insufficient data to make a more positive identification (e.g. Christophel *et al.* 1987; Pole 1992, 1993*c*, 1996; Pole *et al.* 1993). These include for example, several mummified leaves from Mid to Late Eocene sediments at Hasties in north-eastern Tasmania (Pole 1992), two leaf taxa from the Late Oligocene Berwick Quarry in Victoria (Pole *et al.* 1993) and several large leaves in the Early Miocene Manuherikia Group in New Zealand (Pole 1993*b*).

1.3.2 Fossil Pollen Record

Due to the extensive nature of the literature discussing fossil Cunoniaceae pollen it is not the purpose of this summary to collate and interpret it all. Instead, I will discuss the problems associated with the Cunoniaceae pollen record, followed by a review of what pollen types have been recorded and from which geographic regions, and how this has been used to reconstruct palaeoclimates and vegetation. It was beyond the

scope of this study to re-investigate in detail the deposits which have yielded Cunoniaceae pollen as very few fossil samples were available for examination.

1.3.2.1 Limitations Of The Fossil Pollen Record

The primary limitation of the pollen record is its low taxonomic value which is the combined result of several factors; the grains are very small (8-15 μm) and difficult to examine, there has been little research on the features of the pollen grain themselves to enable fine scale taxonomic identifications, and they are similar in appearance to Elaeocarpaceae pollen. Some palynologists do not even distinguish between the pollen of Cunoniaceae and Elaeocarpaceae but rather combine them into a single category or leave the identification unresolved.

As the pollen grains of Cunoniaceae are so small they may have been excluded from some preparations as micro-sieving techniques generally remove fines less than 10 μm in diameter (Sluiter 1991). This problem has been realised and addressed in recent palynological studies but still remains a problem for older studies. Consequently, it must be noted that for older studies the pollen counts may not have detected any Cunoniaceae even though representatives of the family may have been the dominant pollen source in the region.

For Cunoniaceae, most palynologists recognise two broad groups based on colpi number (Table 1.2); dicolp(or)ate and tricolporate. A syncolpate type has been reported in *Gillbeea* (Stover and Partridge 1973; Kershaw and Sluiter 1982). As most records only provide this level of information, for any comparisons to be made between the extant and fossil pollen types it is essential to know which type occurs within each extant genus. This data has not always been consistent, for example Sluiter (1991), Kershaw and Sluiter (1982) and Kershaw (1985) indicate that *Pullea* and *Pseudoweinmannia* have tricolporate pollen, but this determination is not supported by Hideux and Ferguson (1976), M.K. Macphail (pers. com.) and my own observations. Based on a literature review (illustrations of pollen grains) and the data generated from the palynological aspects of this study, the generic distribution of pollen types within the Cunoniaceae is detailed in Table 1.3.

Occasionally, the identification of fossil Cunoniaceae pollen has been at the generic level (e.g. Pocknall 1980; Bakker and Salomons 1989) or generic complex level (e.g. Luly *et al.* 1980; Colhoun *et al.* 1989). These identifications are most common in South America where *Weinmannia* pollen (tricolporate) is relatively abundant in

Table 1.3. Pollen types within the Cunoniaceae

Data without a listed source is from Hideux and Ferguson (1976) and personal observations. The pollen type of all genera was verified during this study.

Pollen type	Genus	Source
Dicolp(or)ate	*Acrophyllum*	
	Anodopetalum	Colhoun (1980), Barnes and Rozefelds (2000, Appendix 1)
	Bauera	Colhoun (1980)
	Callicoma	Kennedy and Prakash (1981)
	Caldcluvia	Heusser (1971)
	Ceratopetalum	Luly *et al.* (1980) Hill and Macphail (1983)
	Eucryphia	Colhoun (1980), Luly *et al.* (1980), Hill and Macphail (1983)
	Geissois	Luly *et al.* (1980)
	Lamanonia	
	Pseudoweinmannia	
	Platylophus	
	Pullea	
	Schizomeria	Kershaw and Sluiter (1982)
Tricolporate	*Ackama*	
	Acsmithia	
	Aistopetalum	
	Codia	
	Cunonia	
	Davidsonia	Watson and Dallwitz (1992)
	Opocunonia	
	Pancheria	
	Spiraeanthemum	
	Spiraeopsis	
	Vesselowskya	Hill and Macphail (1983) Sluiter (1991)
	Weinmannia	Hill and Macphail (1983) Sluiter (1991)
Syncolpate	*Gillbeea*	Stover and Partridge (1973) Kershaw and Sluiter (1982)

Quaternary sediments, with few records of *Caldcluvia* (Heusser 1964) and *Eucryphia* (Godley and Moar 1973; Heusser 1974). The current absence of other Cunoniaceae genera with tricolporate from South America has no doubt aided the identification of tricolporate Cunoniaceae fossil pollen as that of *Weinmannia*. However, in some cases this pollen may equally represent that of another tricolporate genus now extinct from the continent.

Quantitative attempts at distinguishing *Bauera, Anodopetalum* and *Eucryphia* pollen grains from Tasmanian Quaternary sediments have been made by Colhoun (1980) while Luly *et al.* (1980) distinguished between Cunoniaceae pollen in the Oligo-Miocene Yallourn and Morwell Formations on the basis of colpi number and surface ornamentation; tricolporate, dicolporate, *Geissois-Eucryphia* complex and *Ceratopetalum* complex types. Despite these studies, there appears to be no consistency among palynologists when describing fossil Cunoniaceae pollen except for the colpi number. However, even this feature is not always consistent, and is probably due to the little palynological research that has been conducted on this family.

To interpret the pollen record accurately it is beneficial to know the level of representation of the pollen within the fossil bearing sediment compared to that of the extant flora. The representation of Cunoniaceae pollen in the extant flora and fossil record has been investigated by Moar (1970), Pocknall (1978) and McGlone (1982) in New Zealand, Heusser (1974) in Chile, Van der Hammen *et al.* (1980) and Grabandt (1980) in Colombian cloud forests and Bush *et al.* (1990) in Ecuadorian Amazonia. Moar (1970), Pocknall (1978) and McGlone (1982) indicate *Weinmannia*, which is insect pollinated (Pocknall 1978; Van der Hammen *et al.* 1980) and a prolific pollen producer (McGlone 1982), is more or less represented in the modern pollen spectra but under-represented outside the forests where it occurs. This situation is supported by Van der Hammen *et al.* (1980) who illustrated a positive relationship between stands of *Weinmannia* and the presence of their pollen in Colombian surface samples.

These studies suggest that *Weinmannia* at least would be well represented in the pollen record if present in the local flora, but does not contribute to the regional pollen flora or occur in those areas where trees do not actually occur. This conclusion is supported by Bush *et al.* (1990) who examined pollen in sediments from two Ecuadorian Amazonian lakes where *Weinmannia* does not occur in the surrounding vegetation. Only very small amounts of *Weinmannia* pollen was recovered, presumably having travelled relatively long distances. Heusser (1974) also notes that *Weinmannia* and *Caldcluvia-Eucryphia* pollen are proportionally represented in extant Valdivian and

North Patagonian rainforests of Chile. These studies support the view that some genera at least are accurate indicators of the local flora, with little influence from extra-local or regional sources. These studies therefore suggest that the presence and quantity of Cunoniaceae pollen in a sediment would proportionally represent the abundance of Cunoniaceae in the surrounding vegetation.

However, the level of Cunoniaceae pollen can at times be under or overestimated for several reasons. Swamping of *Weinmannia* pollen in the forests dominated by *Quercus* in Colombia (Grabandt 1980) and *Phyllocladus* in New Zealand (Moar 1970) both result in the underestimation of the importance of *Weinmannia* in the surrounding forest. In contrast, Sluiter (1991) suggests that the dominance of tricolporate Cunoniaceae pollen in some Early Cainozoic Australian sediments is artificial and a direct result of the relatively low abundance of Casuarinaceae and *Nothofagus* pollen at this time. Hence, Cunoniaceae pollen may actually be overestimated in some sediments by the nature of the surrounding plants also contributing to the pollen spectra. Therefore, it is not only necessary to consider the pollen count of individual species or genera of Cunoniaceae but also that of other co-occurring taxa that inevitably influence the final calculation of pollen sums and hence pollen representivity.

1.3.2.2 Fossil Pollen Records of Cunoniaceae

The pollen record of Cunoniaceae is temporally widespread with records dating from the Late Paleocene (e.g. Cranwell 1959; Petriella and Archangelsky 1975; Sluiter 1991) and through the Cainozoic (Stover and Partridge 1973; Luly *et al.* 1980; Hill and Macphail 1983; Truswell *et al.* 1985; Christophel *et al.* 1987; Macphail *et al.* 1995). Numerous records are from Quaternary sediments (Moar 1973; Dodson 1978; Pocknall 1980; McGlone and Bathgate 1983; Kershaw 1985; Colhoun and Van de Geer 1986; Markgraf *et al.* 1986; Colhoun *et al.* 1989; Warren 1994), particularly from South America (e.g. Heusser 1964; Schreve-Brinkman 1978; van der Hammen 1978; van der Hammen *et al.* 1980; Villagran 1988; Bakker and Salomons 1989; Bush *et al.* 1990; Hansen *et al.* 1994; van der Hammen and Absy 1994; Hansen and Rodwell 1995; Heusser *et al.* 1995). Fossil Cunoniaceae pollen has been recorded from all Southern Hemisphere continents except for Africa.

Fossil pollen of Cunoniaceae have been used to interpret vegetation history (Heusser 1964; Villagran 1988; Sluiter 1991; Bush *et al.* 1990), regional extinctions (Hill and Macphail 1983), plant migration and dispersal (Truswell *et al.* 1987), palaeoclimatic

estimates (Kershaw and Nix 1988) and glacial events (Heusser 1964; Helmens and Kuhry 1986; Colinvaux *et al.* 1988; Hooghiemstra 1989; Heusser *et al.* 1996).

The pollen record of Cunoniaceae in Australia dates to the Late Paleocene where tricolporate pollen has been recovered from the Lake Eyre region in South Australia (Sluiter 1991). This pollen type enabled the inference that the vegetaion was dominated by important rainforest Cunoniaceae taxa such as *Pseudoweinmannia, Pullea, Caldcluvia* and *Vesselowskya* (Sluiter 1991) which occurred within a simple notophyll vine forest with a minor component of Myrtaceae and conifers. As mentioned previously, the classification of *Pseudoweinmannia* and *Pullea* pollen as tricolporate is considered to be incorrect (see Table 1.2). By the Middle Eocene, tricolporate Cunoniaceae pollen was less common and coincided with the emergence of Myrtaceae, *Nothofagus*, Casuarinaceae, Cunoniaceae (dicolporate), Proteaceae and Restionaceae-Centrolepidaceae as the dominant pollen types. This region now occurs within the semi-arid to arid area of Australia and strongly indicates the Early Cainozoic presence of a climate and vegetation currently extinct in the area.

Similar aged sediments (Late Paleocene) on Seymour Island near the Antarctic Peninsula indicate that a possible Cunoniaceae (cf. *Weinmannia*) or Elaeocarpaceae species occurred within the region at this time (Cranwell 1959) while Paleocene sediments from the Chubut Province in Argentina contain *Rhoipites* sp. which has affinities to *Weinmannia* (Petriella and Archangelsky 1975) and co-occurred with wood identified as the fossil genus *Weinmannioxylon* (see Chapter 6).

An Eocene record of *Concolpites leptos* from the Santa Cruz Province in Argentina (Romero and Castro 1986) is of particular interest as it represents the genus *Gillbeea* which is now restricted to north-eastern Australia and Papua New Guinea (Hoogland 1960). Stover and Partridge (1973) first described this pollen type from the Eocene to Early Oligocene sediments in the Gippsland Basin, Victoria. The next oldest South American record of Cunoniaceae was made by Hooghiemstra (1989) who recorded *Weinmannia* pollen from Upper Pliocene (~ 3.5 Myr) sediments on the Bogotá Plain in Colombia. The lack of any records from sediments aged between these two is probably due to the limited work conducted on many South American Early to Middle Cainozoic deposits rather than a lack of Cunoniaceae in the region during this period.

The New Zealand Cunoniaceae microfossil record is scant, with Romero (1986) noting that the *Weinmannia* pollen type (tricolporate) does not reach New Zealand until the Oligocene, where it has been recorded from Late Oligocene Pomahaka Estuarine

Bed sediments in Southland (Pocknall 1982).

Studies reporting Cunoniaceae pollen in Quaternary and Holocene sediments are very common and have mainly focused on correlating the pollen spectra of modern and fossil assemblages to interpret vegetation change and periods of global cooling. For example, *Eucryphia-Anodopetalum* type pollen has proven to be useful in interpreting the Tasmanian distribution of cool temperate rainforest during the Holocene (e.g. Colhoun and Van de Geer 1986; Markgraf *et al.* 1986). A decline in *Eucryphia-Anodopetalum* pollen in the Quaternary indicated the development of subalpine and alpine shrub vegetation in western Tasmania (Colhoun 1980) while its occurrence in Holocene sediments at Langdon River in western Tasmania support the development of cool temperate rainforest (Colhoun *et al.* 1989).

Quaternary records in the Australian tropics have been reported by Kershaw and Sluiter (1982) and Kershaw (1976, 1985). A Late Quaternary record from Lynch's Crater in north-eastern Australia suggests that the dominance of Cunoniaceae (tricolporate) pollen and *Elaeocarpus* represents the development of complex notophyll or complex mesophyll vine forest during several phases where sclerophyll taxa, such as Casuarinaceae and *Eucalyptus*, were absent or in very low proportions (Kershaw 1985). This was probably during periods of increased effective precipitation and temperature which excluded the 'drier' rainforest types such as Araucarian vine forest. The amount of Cunoniaceae pollen in the Pliocene to Early Pleistocene (c. 5 to 1 Mya) Butchers Creek deposit in north-eastern Australia, compared to that of nearby extant forests, led to the inference that the Butchers Creek fossil spectrum represented that of a submontane rainforest with similar rainfall to current levels (Kershaw and Sluiter 1982).

New Zealand Quaternary records of *Weinmannia* are common (e.g. Dodson 1978; McGlone 1983; McGlone and Bathgate 1983; Mildenhall 1994). Most of these simply document the presence of *Weinmannia* pollen while others interpret its presence as representing phases of vegetation disturbance or glacial retreat (e.g. Moar 1973; Pocknall 1980). Pocknall (1980) suggested that a higher proportion of *Weinmannia* pollen compared to that of *Dacrydium* may represent the lack of any vegetation disturbance to allow the regeneration of *Weinmannia*, which is a process mirrored in the extant vegetation (Wardle 1966).

Quaternary records from South America are abundant, especially from Colombia (Schreve-Brinkman 1978; Van der Hammen 1978; Van der Hammen *et al.* 1980;

Helmens and Kuhry 1986; Bakker and Salomons 1989; Hooghiemstra and Ran 1994), Chile (Heusser 1964; Godley and Moar 1973; Heusser 1974, 1984; Villagran 1988, 1990) and Ecuador (Colinvaux *et al.* 1988; Liu and Colinvaux 1988; Bush *et al.* 1990). *Weinmannia* constitutes most records and has been integral in reconstructing the distribution of Andean cloud forest through the Pleistocene glaciations (e.g. Heusser 1964; Helmens and Kuhry 1986; Colinvaux *et al.* 1988; Bush *et al.* 1990; Villagran 1990; Hooghiemstra and Ran 1994). For example, pollen records from Colombia indicate *Weinmannia* forests have advanced slowly during the wetter Holocene, which suggests that some species at least may need shade and a mature, humic soil to develop and extend their range (Van der Hammen *et al.* 1980). The pollen record has been able to demonstrate the high level of resilience of this taxon to cold and/or glacially dry climates during the Upper Pliocene and Last Glacial at least (e.g. Colinvaux *et al.* 1988; Hooghiemstra 1989).

The pollen record combined with the ranges and survival limits of extant taxa, has enabled the geographic reconstruction of Valdivian and North Patagonian rainforests in Chile (Heusser 1974, 1984; Villagran 1988, 1990) and the identification of periods of glacial retreat and expansion during the Pleistocene and Holocene (Heusser 1964; Heusser 1974; Heusser *et al.* 1995). The association of *Weinmannia trichosperma*, *Caldcluvia paniculata* and *Eucryphia cordifolia* is suggested by Heusser (1974) to represent the presence of Valdivian type rainforest, however Villagran (1993) notes that as each taxon spans various temperature, shade, topographical and moisture gradients, defining their exact implication on vegetation reconstruction is not difficult. However, Heusser (1993) does stress that pollen of *Weinmannia* and others in the Chilotan Archipelago and the Chilean Lake District are good indices of climate change. As with New Zealand, the dominance of *Weinmannia* in glacial sediments (lateral moraine) and a large organic layer has at times be used to allow the inference periods of warm postglacial conditions (Heusser 1964).

Although the Cunoniaceae fossil pollen record is limited by its taxonomic resolution it is informative as it provides evidence for palaeogeographic distributions of pollen types, rather than specific genera. It is reasonable to assume that the presence of Cunoniaceae pollen, and to some extent its dominance, in a fossil sediment does indicate the presence of Cunoniaceae in the nearby vegetation.

Chapter 2. General Materials and Methods

2.1 Plant Specimens And Sampling Methods

As the majority of the Cunoniaceae occur outside Australia it is difficult to obtain fresh or preserved material for examination. Therefore, herbarium specimens, or portions (i.e. individual leaves, leaflets or reproductive structures) of a herbarium specimen were the main source of plant material examined during this study. These were accessed from the Australian National Herbarium (CANB), Herbarium of South Australia (AD), Tasmanian Herbarium (HO), Missouri Botanical Gardens (MO), Atherton Herbarium (QRS) and the University of Minnesota Herbarium (MU). Herbarium material was supplemented with dried or preserved specimens collected by myself or other researchers in the field.

For some genera, fresh leaves, flowers and fruits of some species were readily available from plants propagated at the University of Tasmania (Hobart), the Australian National Botanic Gardens (Canberra), the Royal Tasmanian Botanical Gardens (Hobart) or private gardeners (John Wrigley, New South Wales; Ken Gallanders, Hobart). These included species of mostly Australian genera, such as *Geissois, Ackama, Callicoma, Vesselowskya, Davidsonia, Ceratopetalum, Schizomeria, Anodopetalum, Eucryphia* and *Bauera.* Several *Weinmannia* species (*W. tomentosa, W. trichosperma, W. parviflora, W. sylvicola, W. racemosa*), *Cunonia capensis, Ackama rosaefolia, Pancheria hirsuta* and *Pancheria* sp. indet. were also examined as plants grown from seed or cuttings.

Taxonomic authorities of both extant and fossil species discussed in this study are detailed in Appendix 2. The extant specimens examined in this study are listed in Appendix 3.

Many leaf and floral characters included in this study were examined directly from specimens by eye or with the aid of Zeiss Stemi 2000-C dissecting microscope. For stem and leaf architectural characters, most of the leaves/leaflets of the available specimens were examined, with fine scale venation patterns examined from at least 2 cleared leaves (or leaflets) per species (see technique outlined in 2.2.2 Cleared Leaves, Sepals and Flowers). These leaves were obtained from separate specimens when possible.

Leaf micro-morphological (cuticle) characters were examined from numerous (>3) separate leaves per species. As most samples were obtained from herbarium sheets it was not possible to determine if these represented sun or shade leaves, so to test if these characters were likely to be variable between them, both sun and shade leaves from glasshouse grown plants of several species were examined in detail. The leaves of these species at least were found to be micro-morphologically indistinguishable, as too were the leaves grown in the glasshouse and those grown in the field (i.e. herbarium speicmens). Representative species of each genus were sampled from across their geographic and morphological range where possible, and in some cases, all the species within a genus were examined (e.g. *Ceratopetalum, Ackama, Eucryphia* and *Bauera*). Monotypic genera were sampled more intensively (>3 leaves each from 3 different specimens).

2.2 Leaf and Floral Morphology

2.2.1 Cuticle Preparation

Extant leaf cuticles were prepared from a mid-lamina section of a mature leaf or leaflet placed in 10-30% hydrogen peroxide solution and warmed on a hot plate (30-35 °C) for 24 hours or until all organic matter had oxidised. Several crystals of tetra-sodium pyrophosphate were added to act as a catalyst.

Many of the macrofossils examined in this study preserve organic remains, which is the combined total of the leaf mesophyll, veins and, in most cases, the cuticle. A small quantity of organic remains were removed from selected fossils and treated in 5% hydrofluoric acid (HF) for 24 hours to remove any silica crystals and then rinsed in distilled water. The cuticle was extracted by placing the remains in either a 10-30% hydrogen peroxide solution or a 10% chromium trioxide solution then warmed on a hot plate (30-35 °C) for 24 hours or until all organic matter had oxidised.

For both extant and fossil prepared cuticle, it was rinsed in distilled water and stained with 1% aqueous Safranin O. Cuticles were mounted in phenol glycerine jelly and viewed with a Zeiss Axioskop or Axiolab light microscope.

For scanning electron microscopy, prepared fossil and extant cuticles were placed onto aluminium stubs using double sided carbon tape and allowed to dry prior to

observation with an Environmental Scanning Electron Microscope 2020 (ESEM). To examine the external cuticular features of extant specimens, sections from the mid-lamina region of dried, mature leaves or leaflets were placed directly onto aluminium stubs using double sided carbon tape. For those fossil specimens with delicate cuticle, the organic remains after being treated with HF were placed directly onto the aluminium stubs. For these specimens only the external structures were available for observation with the ESEM. All specimens were either sputter coated with gold and viewed in Hivac mode or viewed in Wet mode, which did not require a gold treatment. The specimens were examined with the ESEM operating at 15-20 kV and a pressure of 0.0 to 8.0 T. The ESEM is housed in the Central Science Laboratory (CSL), University of Tasmania, Hobart.

2.2.2 Cleared Leaves, Sepals and Flowers

Leaves examined in this study were cleared using a modified technique described by Blackburn (1978). Dried or fresh leaves or leaflets were placed in a 10% KOH solution and warmed to 30 °C for 24-48 hours or until the leaf had discoloured and most of the mesophyll had been removed. The solution was changed after 24 hours or when it had become dark brown in colour. The leaves were then washed in 3 rinses of water before being placed in saturated chloral hydrate solution for 24-72 hours or until the leaf had totally cleared and was almost transparent. Cleared leaves were either stored in 70% ETOH or permanently mounted in polyester embedding resin.

For permanent mounting, the leaves were placed through an alcohol series of 10%, 20%, 50%, 90% and 100% ethanol and were then transferred to 100% anhydrous acetone for 30 minutes prior to being placed in uncatylysed embedding resin for a further 30 minutes. The leaves were drained of most of the resin and placed onto a clean glass slide. A mixture of polyester embedding resin and several drops of catylyst (MEKP) was poured over the leaf before another glass slide was pressed onto the leaf. The specimen was weighted with lead weights to ensure the leaves remained flat until the resin hardened, which occurred within 24-72 hours. The slides were cleaned of excess resin by a cloth dampened in acetone.

Whole flowers, fruits and detached sepals of extant species were cleared by placing specimens in 10-50% aqueous hydrogen peroxide solution with several crystals of tetra-sodium pyrophosphate and warming them on a hot plate (30-35 °C) for 24 h or until the venation pattern was clear. Specimens were rinsed in distilled water, stained

in 1% aqueous safranin O and observed with a Zeiss Stemi 2000-C dissecting or Axioskop light microscope.

2.2.3 Pollen Morphology

Pollen grains of representative species of all of the Cunoniaceae genera were examined by crushing a mature anther onto double sided carbon tape on an aluminium stub. These specimens were sputter coated with gold and viewed with an ESEM operating at 15-20 kV in Hivac mode. For species with fresh flowers available, the mature anthers were touched onto the tape rather than crushed onto it as this then reduced the total number of grains on the stub and prevented including any of the anther itself onto the sample, which sometimes obscured the pollen grains.

This above technique was employed to view the number of colpi present in the pollen grains of each genus and the ultra-structure of the exine. Light microscopy was not used as surface details are very difficult to view with this technique and the colpi can often be obscured. As no fossil pollen was being verified as part of this study it was also unnecessary to view the extant pollen with light microscopy for comparisons between extant and extinct grains. This section of the project was conducted to correct the colpi number used by palynologists when describing fossil pollen as Cunoniaceae (see Table 1.3) and to provide data for the cladistic analyses of the family (Bradford and Barnes manuscript submitted, Appendix 1).

2.3 Nomenclature and Terminology

Terminology of leaf venation, architecture and cuticle morphology is in accordance with Hickey (1979), Dilcher (1974) and Stace (1965). Stomatal nomenclature follows Dilcher (1974), with modifications from Baranova (1987).

2.4 Fossil Identification

Historically, palaeobotanists have often applied modern taxonomic names to fossils on the basis of a superficial resemblance to an extant taxon. This has frequently led to the inappropriate application of a modern name to a fossil plant and implies that both are relatively indistinguishable and, by default, may represent that genus or species (see review by Collinson 1986). In some cases this may be valid, however for old fossil

specimens (>1 Mya) it is unlikely that it does represent the extant species. This has led to the proposal that all fossil plants be assigned unique names that are quite distinct from those of extant genera to avoid the problems of indicating taxonomic affiliation. However, this technique is rejected as it does not allow for a potential taxonomic relationship to exist between living and fossil plants, which is almost certainly the case.

A relatively recent palaeobotanical technique is to examine the architecture of the specimen in addition to any micromorphological structures, if preserved. Dilcher (1974) describes in detail the use of venation and micro-morphological (cuticular) features in identifying fossil plant remains. This technique is based on the detailed examination of extant specimens to which the fossil appears to be most similar. In most cases, leaf and micromorphological data has not been documented for extant genera and species as traditional taxonomy is almost solely based on floral rather than leaf morphology. In this respect, many useful taxonomic characters to delineate families, genera and species have gone undetected.

In this study, the fossil specimens are examined to the fullest extent, extracting as much data as the fossil will permit. For example, mummified leaves preserve more data in the form of leaf cuticle, than do leaf impressions where there is no organic remains. Comparisons between the morphological structures and features of both fossil and living specimens are made. In the case of dispersed organs, the conservative approach is adopted whereby separate names are applied to each organ. In some cases the dispersed organs may have arisen from the same plant, but in the absence of an organic connection it cannot be confirmed. This approach may cause unnecessary name generation in some instances but it is the usual procedure of modern palaeobotanists and it must be recognised that names assigned to some fossil species in this study may become redundant if specimens are located with an organic connection.

2.5 Fossil Localities, Geological Ages and Specimens

Most of the fossil specimens examined in this study have been collected or extracted from Australian Cainozoic sediments for other studies (e.g. Carpenter and Buchanan 1993; Pole *et al.* 1993). In addition to these specimens, numerous leaf and reproductive structures of Cunoniaceae were extracted from some Australian Cainozoic deposits and are described here for the first time. Attempts to locate some specimens, particularly those described in the older literature (e.g. Milligan 1849; Ettingshausen

1888), were in most cases unsuccessful, even after contacting the institutions where many were believed to be housed. Many of these latter specimens may be lost. The location of Australian and New Zealand fossil deposits are shown in figures 2.1 and 2.2.

This section does not list all the references for each fossiliferous deposit, but rather details some of the key references that age the deposit, the macroflora it contains and the fossils or illustrations of the fossils examined during this study from each deposit. Some of the minor deposits where there is scant information on deposit age and macroflora composition are not presented in this chapter, but are instead discussed in the relevant chapter. Deposits are arranged alphabetically, and generally the prefix for each fossil specimen denotes the code used to identify that particular deposit. For example, WC identifies the fossil as being extracted from the Wilsons Creek deposit in central Tasmania.

2.5.1 Berwick Quarry, Victoria

The Berwick Quarry macroflora is preserved in buff to chocolate brown muds which are Late Oligocene to possibly earliest Early Miocene in age (Pole *et al.* 1993). Deane (1902*a*) described several species from this locality, including species of *Eucalyptus* (Myrtaceae), *Lomatia* (Proteaceae), *Atherosperma* (Monimiaceae), *Fagus* (Fagaceae) and *Aristotelia* (Tiliaceae). All the identifications by Deane (1902*a*) were based on gross morphology only.

An examination of new collections from the site by Pole *et al.* (1993) yielded leaves of rainforest taxa (Lauraceae, *Nothofagus, Agathis*, *Dacrycarpus* and *Gymnostoma*) and *Eucalyptus*. This combination of taxa was interpreted by Pole *et al.* (1993) to be evidence of both rainforest and open forest vegetation, possibly indicative of drought events and general cooling. Pole *et al.* (1993) considered several of Deane's (1902*a*) *Lomatia* species to be 'probably Cunoniaceae' and also described three new leaf macrofossils as ?Cunoniaceae sp. '*Callicoma*'. Specimens are housed in the Department of Environmental Biology, University of Adelaide.

Specimens examined:

?Cunoniaceae sp. '*Callicoma*' (Pole *et al.* 1993; Chapter 4)

SB-220, 315, 319

Fig. 2.1. Map of mainland Australia and Tasmania (inset) showing the fossil localities included in this study.

Localities marked with an asterix have not had Cunoniaceae macrofossils described from them and are not discussed at length in this study. They are mentioned as they contain a rich diversity of Elaeocarpaceae leaf macrofossils (e.g. Christophel and Greenwood 1987).

Refer to '2.5 Fossil Localities, Geological Ages and Specimens' for site descriptions and previous research that has been conducted on each deposit.

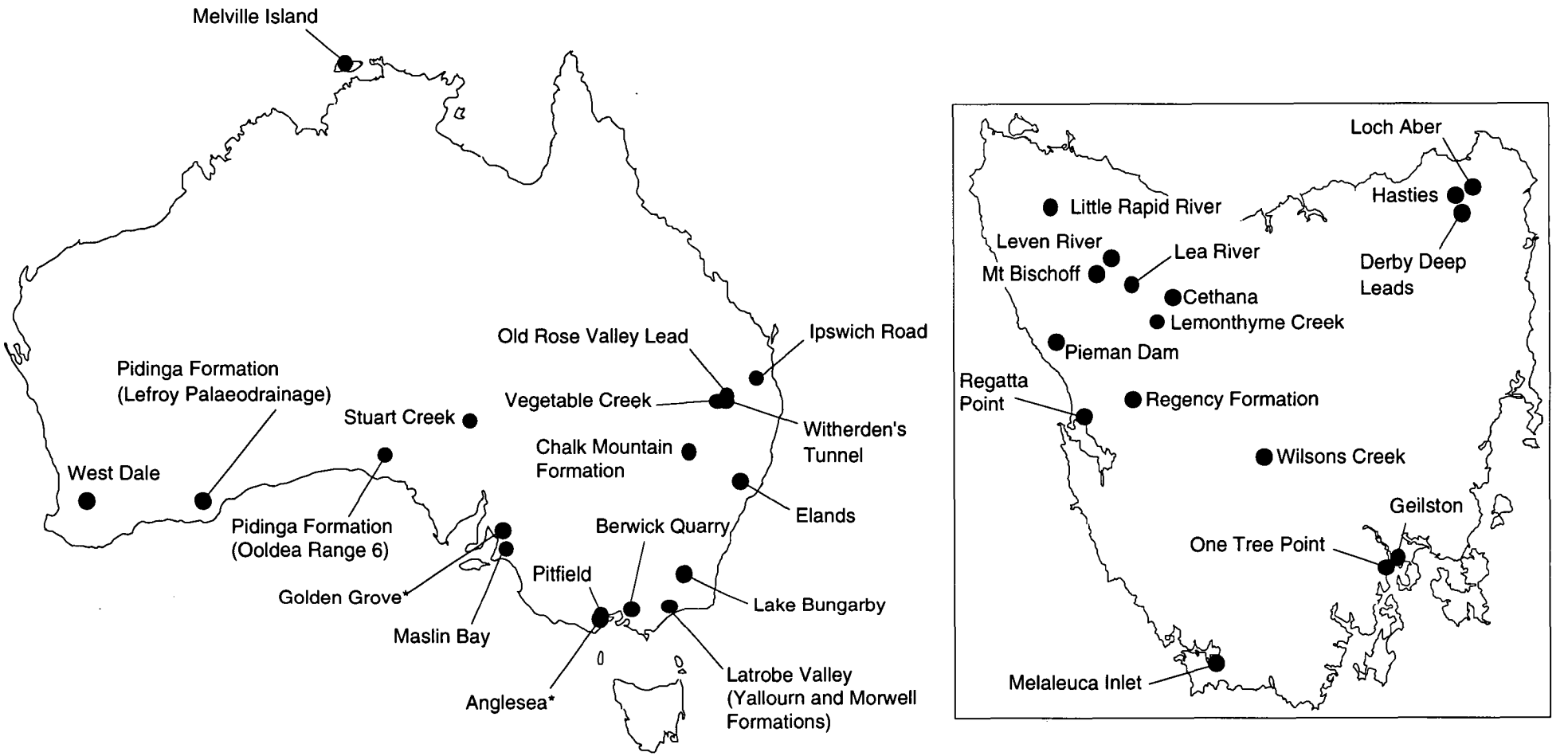
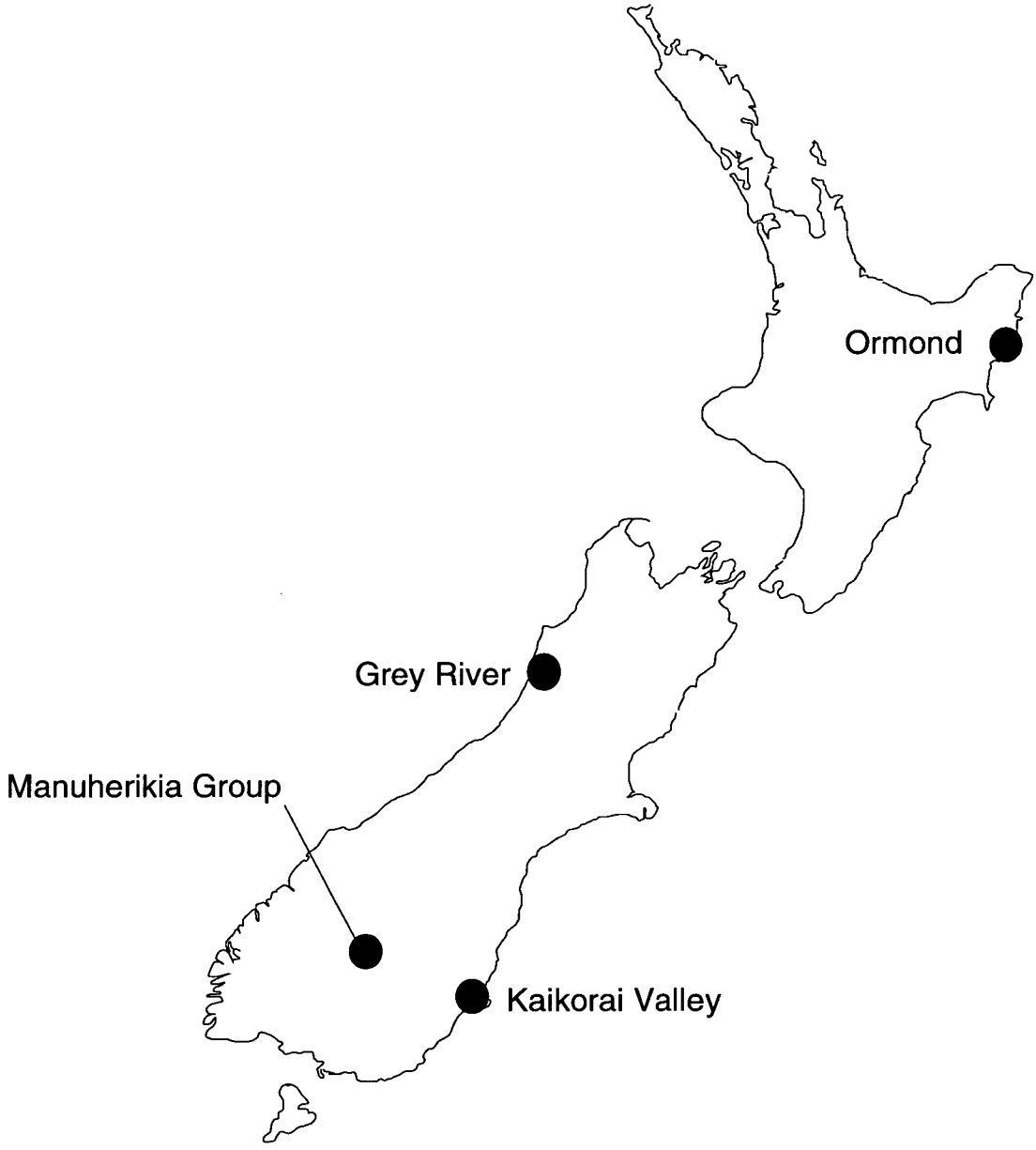

Melville Island
Old Rose Valley Lead
Ipswich Road
Pidinga Formation
(Lefroy Palaeodrainage)
Vegetable Creek
Stuart Creek
Witherden's
Tunnel
Chalk Mountain
Formation
West Dale
Elands
Pidinga Formation
(Ooldea Range 6)
Berwick Quarry
Pitfield
Golden Grove*
Lake Bungarby
Maslin Bay
Latrobe Valley
(Yallourn and Morwell
Formations)
Anglesea*
Loch Aber
Hasties
Little Rapid River
Leven River
Lea River
Derby Deep
Leads
Mt Bischoff
Cethana
Lemonthyme Creek
Pieman Dam
Regatta
Point
Regency Formation
Wilsons Creek
Geilston
One Tree Point
Melaleuca Inlet

Fig. 2.2. Map of New Zealand showing the fossil localities included in this study.

Refer to '2.5 Fossil Localities, Geological Ages and Specimens' for site descriptions and previous research that has been conducted on each deposit.


Ormond
Grey River
Manuherikia Group
Kaikorai Valley

?Cunoniaceae sp. 'lanceolate' (Pole *et al.* 1993; Chapter 6)

SB-292, 210, 217-219, 222-225, 228, 230, 231, 234, 235, 239, 243, 250, 251, 261, 263, 264, 284-287, 292-303, 306, 308, 310-314, 316, 322, 324, 324

?Cunoniaceae sp. 'small teeth' (Pole *et al.* 1993; Chapter 6)

SB- 309, 317

2.5.2 Cethana, north-central Tasmania

The macrofossils and palynology of the Early Oligocene Cethana deposit (Carpenter and Hill 1988) in north-central Tasmania have been extensively studied (e.g. Hill 1984*a*; Carpenter and Hill 1988; Carpenter 1991 *a, b*; Carpenter and Buchanan 1993; Carpenter and Jordan 1997). The macrofossils include taxa with nearest living relatives in micro- and meso-thermal habitats of the Australian-Pacific region such as ferns, cycads, conifers (e.g. *Dacrycarpus, Acmopyle, Papuacedrus, Agathis* and *Araucaria*), *Nothofagus*, Lauraceae and Cunoniaceae (e.g. Hill 1984*a*; Carpenter 1991 *a, b*; Carpenter and Jordan 1997).

A single specimen each of a leaf and infructescence of *Callicoma serratifolia* have been described by Carpenter and Buchanan (1993) which occurred with other Cunoniaceae macrofossils (e.g. *Schizomeria, Vesselowskya* and *Weinmanniaphyllum*). All the specimens described by Carpenter and Buchanan (1993) were available for this study. These were supplemented by additional leaf specimens located in Cethana sediment stored at the School of Plant Science, University of Tasmania.

Specimens examined:

Acsmithia grandiflora (Carpenter and Buchanan 1993; Chapter 6)

C-736 (holotype), 737

Callicoma serratifolia (Carpenter and Buchanan 1993; Chapter 4)

C-480, 531, 1017, 1019-1022

Schizomeria tasmaniensis (Carpenter and Buchanan 1993; Chapter 6)

C- 501 and counterpart (holotype)

Vesselowskya aff. *rubifolia* (Carpenter and Buchanan 1993; Chapter 6)

C-621

Weinmanniaphyllum bernardii (Carpenter and Buchanan 1993; Chapter 6)

C-033, 060, 138, 356, 377 (holotype), 638, 639, 645, 663, 664

2.5.3 Chalk Mountain Formation, New South Wales

The Chalk Mountain Formation is a lacustrine deposit interbedded between basalt flows that are of Middle Miocene age (see Holmes and Holmes 1992). The macroflora has been discussed by Holmes *et al.* (1983) and Holmes and Holmes (1992) but only two genera (*Eucalyptus* and *Ceratopetalum*) have been formally identified from the deposit. Holmes and Holmes (1992) described three fruits preserved in the diatomite as the single species *Ceratopetalum priscum* and probably grew in association with rainforest and sclerophyllous elements (see Holmes *et al.* 1983). The illustration and species description from Holmes and Holmes (1992) were available for this study. An illustration of a paratype was also available (White 1990, p. 197).

Specimens examined (illustrations and descriptions only):

Ceratopetalum priscum (Holmes and Holmes 1992; Chapter 3)

MMF25501 (holotype)

Ceratopetalum priscum (White 1990)

AMF3975 (paratype)

2.5.4 Derby Deep Leads, north-eastern Tasmania

Scott (ca. 1937) identified wood as *Ceratopetalum clarkii* Scott from this Early Tertiary deposit in north-eastern Tasmania. The fossil deposit is described by Scott (ca. 1937) to have been located 500 feet below basalt of Miocene age in the Brieseis Mine. Sections of the fossil wood were produced and examined by Scott (ca. 1937) but he provides no reference numbers to those specimens he considered to be *C. clarkii.* Jordan and Hill (1998) have reported that the locality has been permanently flooded and that all the fossiliferous material has probably been removed during open cut mining activities in the area. No previously collected specimens were located. The unpublished report of Scott (ca. 1937) was available for this study.

Specimens examined (description only):

Ceratopetalum clarkii (Scott ca. 1937; Chapter 3)

- no reference numbers

2.5.5 Elands, north-eastern New South Wales

The late Early-Late Miocene Elands locality has been described by Hill and Whang (2000). A single, organic fruit that can be assigned to extant *Ceratopetalum* has been extracted from very thin (approx. 1 mm) laminated pale siltstone. The fossil fruit occurs in sediment with leaves and reproductive organs of *Eucalyptus*. Other layers contain *Dacrycarpus, Eucalyptus*, numerous unidentified angiosperms and ferns. These taxa indicate rainforest vegetation with wet sclerophyll elements and *Eucalyptus* either intermixed or in close proximity spatially and/or temporally. One specimen is housed in the School of Plant Science, University of Tasmania.

Specimens examined:

Ceratopetalum westermannii (Chapter 3)

ELD-20 and counterpart (holotype), 21

2.5.6 Geilston, south-eastern Tasmania

This limestone deposit is at least Oligocene in age, or possibly older, and preserves leaves and fruit (Tedford *et al.* 1975). Jordan and Hill (1998) consider the site to represent Johnston's (1887) "Risdon" site from which he describes several conifers, *Fagus* (=*Nothofagus*), and various broad leaf angiosperms. Ettingshausen (1888) described *Ceratopetalum woodii* Ett. from this locality, in addition to other taxa including *Araucaria, Cinnamomum* and *Fagus risdoniana.* The deposit is now located under a permanent building and is uncollectable (Jordan and Hill 1998). The illustration and description of *C. woodii* by Ettingshausen (1888) was available for this study but the original specimen could not be located.

Specimens examined (illustration and description only):

Ceratopetalum woodii (Chapter 3)

2.5.7 Grey River, New Zealand

Ettingshausen (1890) described this site as containing many but not very well preserved leaf macrofossils. Species described from the locality include *Flabellaria longirachis*, two species of *Quercus, Celastrophyllum, Palaeocassia, Knightiophyllum* and a species of *Ceratopetalum, C. rivulare* Ett. (Ettingshausen 1890). The illustration

and description of *C. rivulare* by Ettingshausen (1888) was available for this study but the original specimen could not be located.

Specimens examined (illustration and description only):

Ceratopetalum rivulare (Chapter 3)

2.5.8 Hasties, north-eastern Tasmania

Pole (1992) has described the macroflora from this Mid-Late Eocene deposit in north-eastern Tasmania. The assemblage includes numerous conifers species of the families Podocarpaceae (*Dacrycarpus, Podocarpus, Phyllocladus* and *Prumnopitys*), Araucariaceae (*Araucaria* spp.), Myrtaceae (cf. *Xanthomyrtus*), Nothofagaceae (*Nothofagus tasmanica*), Lauraceae (*Laurophyllum* sp.), Casuarinaceae (*Gymnostoma* sp.) and Proteaceae (*Cenarrhenes nitida*). The vegetation probably grew in a floodplain basin swamp with a high rainfall and cool seasonal climate (Pole 1992).

Several incomplete leaves have been extracted and assigned to the family Cunoniaceae by Pole (1992). The very small leaves are described by Pole (1992) to possess a serrate margin and general cuticle, whereby there are no or few distinguishing features. A single specimen was available for a detailed examination during this study, while illustrations and descriptions of all other specimens were available from Pole (1992). Specimens are housed in the Queen Victoria Museum (QVM), Tasmania.

Specimens examined (one specimen examined in detail, others by description and illustration only):

?Cunoniaceae Genus et species indet. (Chapter 6)

SB-132 (specimen), SB-133, S157, QVM:1989:GFP:001-QVM:1989:GFP:006

2.5.9 Ipswich Road, Queensland

There is scant information on this fossil deposit. Ettingshausen (1894) describes the deposit as Tertiary, in accordance with most of the other fossiliferous deposits he studied (e.g. Ettingshausen 1888). Species of *Fagus, Laurus, Cassia* and *Eucalyptus*, and a single species of *Ceratopetalum, C. primigenium*, were described by Ettingshausen (1894). The illustration and description of *C. primigenium* were

available for this study but the original specimens could not be located.

Specimens examined (illustration and description only):

Ceratopetalum primigenium (Chapter 3)

2.5.10 Kaikorai Valley, New Zealand

Oliver (1936) considered this site to be Pliocene in age, primarily on the affinities of the macroflora to similarly aged deposits within New Zealand, and the geological evidence provided by Benson (1959 cited in Pocknall and Tremain 1988). Since this time, Pocknall and Tremain (1988) have indicated that the deposit is Late Miocene age (Taranaki Series) based on palynological data. This latter age has received support from radiometric dates of two nearby Dunedin volcanic flows of 13.1±0.1 Ma and 10.1±0.2 Ma (McDougall and Coombs 1973).

The macroflora, as described by Oliver (1936), contained *Parafagus, Fagus, Laurelia, Coprosma, Nothopanax* and a single species of *Ceratopetalum, C. kaikoraiense.* Campbell (1985) has more recently reassigned the *Parafagus* and *Fagus* macrofossils to *Nothofagaphyllites* to highlight affinities to the extant genus *Nothofagus.* The palynomorph spectra (see Pocknall and Tremain 1988) includes ferns (*Dicksonia* and *Cyathea*), conifers (*Dacrycarpus, Dacrydium* and *Phyllocladus*), Compositae, *Weinmannia, Leptospermum, Metrosideros* and *Nothofagus.* The illustration and description of *C. kaikoraiense* by Oliver (1936) were used in this study as the original specimen could not be located.

Specimens examined (illustration and description only):

Ceratopetalum kaikoraiense (Chapter 3)

2.5.11 King George Island (South Shetlands), Antarctica

Several fossil deposits occur on King George Island in Antarctica. The Fossil Hill Formation is of Middle to Late Eocene age based on the macroflora present (Czajkowski and Rosler 1986) and the isotopic dates (52±1-43±2 Mya) provided by Zhaonai *et al.* (1989). One of the fossils in this deposit was considered by Dusén (1908) to represent a stipule of *Caldcluvia*, and named it *C. mirabilis.* Czajkowski and Rosler 1986) later assigned leaf macrofossils to this species from the same sediments.

Other macrofossils in the deposit included leaves of *Nothofagus* (Li 1994), *Myrica, Saxegothopsis, Fitzroya*, and numerous fern species (Czajkowski and Rosler 1986). The descriptions and illustrations of *C. mirabilis* by Czajkowski and Rosler (1986) were examined in this study as the original specimens could not be located.

Fossil wood collected from near the Collins Glacier on King George Island has been described as *Caldcluvioxylon collinsense* (Shanzhen and Qingzhi 1994). The wood was compared to that of the extant genus *Caldcluvia*. The descriptions and illustrations of *C. collinsense* by Shanzhen and Qingzhi (1994) were available for this study.

Specimens examined (illustrations and descriptions only):

Caldcluvia mirabilis (Fossil Hill Formation; Chapter 6)
Caldcluvia ?mirabilis (Fossil Hill Formation; Chapter 6)
Caldcluvioxylon collinsense (Collins Glacier; Chapter 6)

2.5.12 Lake Bungarby, New South Wales

Taylor *et al.* (1990) have extensively described the stratigraphy of the Lake Bungarby locality, assigning the palynoflora to the Upper *Lygistepollenites balmei* Zone (Stover and Partridge 1973), which corresponds to the Late Paleocene. The macroflora at the site has not been extensively studied, with most emphasis given to the conifers. The locality preserves foliage of *Acmopyle* (Hill and Carpenter 1991), species of Cupressaceae (Whang and Hill 1999), *Banksieaephyllum taylori* (Carpenter *et al.* 1994) and *Eucryphia falcata* (Hill 1991*a*). Taylor *et al.* (1990) describe the palaeoclimate as having temperature ranges between 14 and 20 °C with little evidence that frosts were significant. Tree ring structure supports this latter hypothesis and further indicates that the climate was markedly seasonal, with a distinct non-growing season (Taylor *et al.* 1990). The specimens described as *E. falcata* by Hill (1991*a*) were available for this study. Specimens are housed in the Department of Environmental Biology, University of Adelaide.

Specimens examined:

Eucryphia falcata (Chapter 5)
LB-025 (holotype), 066, 098, 103, 134

2.5.13 Lea River, north-western Tasmania

This locality in north-western Tasmania has been palynostratigraphically aged as Early Oligocene (M. K. Macphail pers. com.). The deposit contains abundant, well preserved mummified leaves, fruits, twigs and wood and included Proteaceae (Jordan *et al.* 1998), Cupressaceae (Hill *et al.* 1993; Hill and Whang 1996) and *Nothofagus* (Whang and Hill 1995; Scriven and Hill 1996) but also many undescribed taxa. A single fossil capsule assignable to *Eucryphia* was extracted from macerated sediment. The *Eucryphia* specimens from this site are housed in the School of Plant Science, University of Tasmania.

Specimens examined:

Eucryphia reticulata (Chapter 5)

Lea-3301 (holotype)

2.5.14 Lemonthyme Creek core, north-western Tasmania

The age and stratigraphy of the Lemonthyme Creek core have been described by Macphail *et al.* (1993*a*). Palynological data indicates an Early Oligocene age with age limits set to the latest Eocene and earliest Oligocene (see Macphail *et al.* 1993*a*). Jordan *et al.* (1998) have described four leaf macrofossils from the core as Proteaceae species of the fossil genus *Euproteaciphyllum.* Three incomplete coalified leaf compressions of *Callicoma* have been located within the core and were available for this study. These three specimens are housed in the Department of Environmental Biology, University of Adelaide.

Specimens examined:

Callicoma serratifolia (Chapter 4)

LT-67 (and counterpart, LT-68), 162, 1000.

2.5.15 Leven River, north-western Tasmania

Based on palynostratigraphy, this locality in north-western Tasmania is Early Oligocene in age (Carpenter and Jordan 1997; Jordan *et al.* 1998) and contains mummified leaves, wood and twigs. A single species of Proteaceae, *Orites excelsoides* R.J.Carp. & G.J.Jord., has been described from the sediment which also

contains *Nothofagus, Eucryphia*, other angiosperms and at least four imbricate conifer species (Carpenter and Jordan 1997).

Macerate was prepared by soaking blocks of sediment in 10% hydrofluoric acid for 2-4 weeks then rinsing with water to dissociate the sediment and macrofossils. The numerous leaf fragments that were extracted and examined from the macerate did not represent *Eucryphia*, so it is only known from the locality as dispersed cuticle. This cuticle was previously located and prepared by R. J. Carpenter and was available for this study. Slide specimens are housed at the School of Plant Science, University of Tasmania.

Specimens examined:

Eucryphia indet. sp. dispersed cuticle

Lev-100 (slides with cuticle fragments)

2.5.16 Little Rapid River, north-western Tasmania

Macrofossils from this Early Oligocene (Macphail *et al.* 1994) deposit in north-western Tasmania have been described by several authors (e.g. Hill 1987; Hill and Carpenter 1989; Hill and Scriven 1997). Mummified leaves and reproductive structures are preserved in coarse sands and include several subgenera of *Nothofagus* (see Hill 1987, 1991*b*), Lauraceae, *Gymnostoma* (Hill and Scriven 1997) and a large diversity of conifers (see Hill 1995). Several leaves, leaf fragments and two infructescences which were assignable to *Callicoma serratifolia* were examined during this study in addition to several leaf fragments and a capsule assignable to *Eucryphia.* Specimens are housed in the Department of Environmental Biology, University of Adelaide.

Specimens examined:

Callicoma serratifolia leaves and leaf fragments (Chapter 4)

LRR1-1648, 3000-3003, 3005-3009, 3013, 3016-3020

Callicoma serratifolia infructescences (Chapter 4)

LRR1-3015, 4054

Eucryphia aberensis (Chapter 5)

LRR1-4010, 4011, 4013-4014, 4016-4017, 4019-4020, 4022-4028, 4030-4045, 4047-4052, 4057

Eucryphia sp. incomplete capsule (Chapter 5)

LRR1-4046

2.5.17 Loch Aber, north-eastern Tasmania

This locality is Middle to Late Eocene in age based on M.K. Macphail's (in Hill and Christophel 1988) assignment of the palynoflora to the Lower *Nothofagidites asperus* Zone of Stover and Partridge (1973). It contains a diverse fossil flora including mummified leaves, leaf fragments, wood and reproductive organs, though only *Eucryphia aberensis* (Hill 1991*a*), *Banksieaephyllum attenuatum* (Hill and Christophel 1988), and six species of conifer (Hill 1989, 1990; Hill and Carpenter 1991; Pole 1992) have been formally described from this site. The specimens of *E. aberensis* that were examined by Hill (1991*a*) were available for this study in addition to specimens from more recent collections of the locality. An emended diagnosis for *E. aberensis* is presented. Specimens are housed in the Department of Environmental Biology, University of Adelaide.

Specimens examined:

Eucryphia aberensis leaves and leaf fragments (Chapter 5)

LA-009, 013 (holotype), 018, 029, 048, 212, 220, 222, 223-229, 235-236, 238-247

2.5.18 Maslin Bay, South Australia

The Maslin Bay macroflora was preserved in a carbonaceous clay lens and has a Middle Eocene age (Alley 1987; Lindsay and Alley 1995). The macrofossils have been the subject of several investigations (e.g. Christophel and Blackburn 1978; Blackburn 1981; Alley 1987; Scriven 1993; Scriven and Christophel 1990).

A single fruit illustrated by Christophel and Blackburn (1978) has been suggested to represent *Ceratopetalum* (e.g. Holmes and Holmes 1992; see Christophel 1994) but was never formally described. The specimen illustrated by Christophel and Blackburn (1978) could not be relocated but six other specimens were available for this study. Specimens are housed in the Department of Environmental Biology, University of Adelaide.

Specimens examined:

Ceratopetalum maslinensis fruits (Chapter 3)

S-1786, S-840, S-1700, S-6001 (holotype), S-6002.

2.5.19 Melville Island, Northern Territory

This site has been discussed by White (1974) and Pole and Bowman (1996). White (1974) described species of Proteaceae, Elaeocarpaceae and Cunoniaceae from the deposit and suggested it is Eocene-Recent in age. Pole and Bowman (1996) re-collected fossiliferous material from the locality and re-appraised the work of White (1974). They considered many of White's (1974) identifications to be invalid as the fossil material was too fragmentary or lacked any diagnostic features for meaningful comparisons to be made with extant taxa. Pole and Bowman (1996) described Cupressaceae, Proteaceae (*Grevillea* and cf. *Dilobia*) and *Melaleuca* (Myrtaceae) from the sediment and redefined the age of the deposit as Tertiary. The macroflora indicates that the area of deposition was surrounded by a non-rainforest vegetation with possibly seasonal rainfall (Pole and Bowman 1996).

White (1974) described specimen CPC 17128 as '*Ceratopetalum*' with possible affinities to Ettingshausen's (1888) *C. macdonaldi* from Witherden's Tunnel (see below site description). The illustration and description by White (1974) were available for this study in addition to the illustrations provided by Pole and Bowman (1996).

Specimens examined:

Ceratopetalum cf. *macdonadli* (Chapter 3)

2.5.20 Morwell Formation, Latrobe Valley, Victoria

The micro- and macrofossils and stratigraphy of the Morwell Formation in south-eastern Australia have been described by various authors (e.g. Deane 1925; Blackburn 1985; Blackburn and Sluiter 1994 and authors cited therein). The coal has an Oligocene-Early Miocene age and was formed under swamp conditions as indicated by the presence of different colour lithotypes (Blackburn and Sluiter 1994). Families represented within the deposit by micro- or macrofossils include Myrtaceae, *Nothofagus* (*Nothofagidites* pollen type), Casuarinaceae (*Gymnostoma*), Proteaceae, Podocarpaceae (*Dacrycarpus* and *Podocarpus*), Saxifragaceae (*Quintinia*), Araucariaceae (*Araucaria* and *Agathis*), Elaeocarpaceae and Cunoniaceae (Blackburn and Sluiter 1994 and authors cited therein). This deposit is overlain by the younger Yallourn Formation (see 2.5.36 Yallourn Formation, Latrobe Valley, Victoria).

Blackburn (1985) has described dispersed cuticle as Cunoniaceae aff. *Callicoma* (Taxon 27) from a single sample of medium light lithotype based on the sunken stomata occurring in areoles and the subsidiary cell arrangement. Cookson and Duigan (1950) record *Phyllites yallournensis* from this deposit that was first described from the Yallourn Formation (type locality). The fossil has a superficial resemblance to leaves of Banksineae (Proteaceae), but was shown by Cookson and Duigan (1950) to be distinct from this family but they offered no suitably alternative affinities. Blackburn (1985) suggested that the affinities of *P. yallournensis* lie with the Cunoniaceae based on leaf and epidermal morphology. This was accepted by Blackburn and Sluiter (1994) in a detailed revision of the palaeobotany of the Latrobe Valley Coal flora, yet was not based on any evidence provided by comparisons with the extant Cunoniaceae flora. The descriptions and illustrations by Blackburn (1985) and Cookson and Duigan (1950) were available for this study.

Specimens examined (descriptions and illustrations only):

Cunoniaceae aff. *Callicoma* dispersed cuticle (Chapter 4)

Taxon 27 (plate 25 c, d and e in Blackburn 1985).

Phyllites yallournensis (Chapter 6)

N.M.V. 14777, 14778, 14779

2.5.21 Mt Bischoff, north-western Tasmania

Carbonaceous siltstones are reported to occur at the base of Waratah Falls in north-western Tasmania (Everard 1989, cited in Jordan and Hill 1998). Microfossils indicate a Late Oligocene to Early Miocene age (Harris 1968 and 1973, cited in Jordan and Hill 1998), with a more recent and detailed palynological study supporting an Early to Late Oligocene age (S. M. Forsyth, pers. comm. to Jordan and Hill 1998). Johnston (1887) described *Eucalyptus, Laurus, Quercus, Ulmus* and *Taxites* species from the deposit. Other leaf forms in the deposit were considered by Ettingshausen to approach those in the fossil deposits at Breadalbane and One Tree Point (see description below), with particular reference to the genera *Ceratopetalum, Lomatia* and *Ficonium* (see Johnston 1885).

Specimens examined (no illustrations or descriptions located):

?*Ceratopetalum* sp. (Chapter 3)

2.5.22 Old Rose Valley Lead, near Emmaville, N.S.W.

A single fruit from the Late Eocene-Early Oligocene (Picket *et al.* 1990) Vegetable Creek Deep Leads in northern New South Wales was extracted and identified as *Getonites wilkinsonii* Ett. by Ettingshausen (1888). Ettingshausen (1888) believed that this fossil belonged to the Combretaceae, but he could not assign the fossil to an extant genus, so the fossil genus *Getonites* Ett. was erected, with reference to its similarities to *Getonia floribunda* (now *Calycopteris floribunda* (Roxb) Lam.). Holmes and Holmes (1992) considered the specimen more representative of *Ceratopetalum* so re-assigned it to *C. wilkinsonii.* The illustrations and descriptions by Ettingshausen (1888) and Holmes and Holmes (1992) were available for this study.

Specimens examined (illustrations and descriptions only):

Ceratopetalum wilkinsonii (Chapter 3)

MMF8812 (holotype)

2.5.23 One Tree Point, south-eastern Tasmania

This locality is described as Early Tertiary by Ettingshausen (1888). Impressions of leaves and fruits occur in laminated mudstones under basalt, which is the main basis for the Early Tertiary age (Jordan and Hill 1998). Ettingshausen (1888) described *Ceratopetalum woodii* Ett. from this locality in addition to others, including *Betula derwentiensis, Cassia flindersii, Lomatia praelongifolia, Dryandroides johnstonii* and several *Phyllites* species. The original specimens examined by Ettingshausen (1888) could not be located but the description and illustration were available for this study.
Specimens examined (illustration and description only):

Ceratopetalum woodii (Chapter 3)

2.5.24 Ormond (Waipoa Series), New Zealand

Oliver (1928) described this locality as Later Pliocene in age, based mainly on the presence of the mollusc *Acteon sulcatus* (Hutt.). The presence of extinct New Zealand taxa within the deposit and many similar to those described by Ettingshausen (1888) from Early Tertiary deposits within Australia lead Oliver (1928) to the inference that the deposit age was not younger than Later Pliocene. The site preserves carbonised

remains and impressions of leaves and several seed cases within fine grained volcanic silt. A single incomplete specimen has been assigned to the species *Ceratopetalum pacificum* Oliver (Oliver 1928). The illustration and description of *C. pacificum* by Oliver (1928) were used in this study as the original specimen could not be located.

Specimens examined (illustration and description only):

Ceratopetalum pacificum (Chapter 3)

2.5.25 Pidinga Formation, southern Australia

Cores sampling the Pidinga Formation have yielded sediments containing both micro- and macrofossils (Alley and Benbow 1989; Carpenter and Pole 1995). The Formation extends from South Australia to Western Australia across the Nullabor Plain, with its stratigraphy discussed by Clarke (1993) and Alley and Benbow (1989).

Carpenter and Pole (1995) examined the dispersed cuticle and other organic remains from cores of the Lefroy and Cowan palaeodrainages (Middle Eocene) in Western Australia. Taxa present included *Gymnostoma* (Casuarinaceae), *Nothofagus*, Cupressaceae, Araucariaceae (*Agathis*), Podocarpaceae (*Dacrycarpus, Dacrydium, Acmopyle*), Lauraceae, Myrtaceae, and Proteaceae (see Carpenter and Pole 1995). Dispersed cuticle with affinities to *Spiraeanthemum/Acsmithia* was recorded from the Lefroy paleodrainage core (Carpenter and Pole 1995).

Another core of the Pidinga Formation was taken at the Ooldea Range in western South Australia. The palynology and stratigraphy of the Ooldea Range 6 core has been well discussed by Alley and Benbow (1989) and authors cited therein. The sediments are considered to have formed under a marginal marine setting, perhaps on the landward side of an estuary or a lagoon (Alley and Benbow 1989). Comparisons of the palynostratigraphy with other palynofloras suggests a late Middle Eocene to early Late Eocene age (Alley and Benbow 1989). Dr Andy Rowett (Department of Mines and Energy, South Australia) has extracted dispersed cuticle from this core, with several fragments having potential affinities to the cuticle of extant *Spiraeanthemum* or *Acsmithia*. Photographs of these cuticle fragments were available for this study.

Specimens examined (illustrations and descriptions only):

Spireaenthemum/Acsmithia (Carpenter and Pole 1995; Chapter 6)

SB-448 (sample reference CD2999, 38 m; Cut-Z-002)

Dispersed cuticle (Ooldea Range 6; Chapter 6)

OR1-012

2.5.26 Pieman Dam site, north-western Tasmania

The stratigraphy of the Pieman Dam site has been well discussed by Colhoun (1980). The age of the deposit is Middle or Late Pleistocene (> 54, 000 years B.P. based on 14C dating, Colhoun 1980). The macroflora contains very well preserved leaves of extant Tasmanian rainforest species such as *Nothofagus cunninghamii* and *Eucryphia lucida*. No original specimens were available for this study.

2.5.27 Pitfield, Victoria

The deposit, located in southern Victoria, is accessed from a bore approximately 100 ft below the surface and is overlain by two distinct layers of basalt and underlain by basalt (Deane 1902*b*, *c*), and has been discussed by Deane (1902*b*, *c*). The vegetation was described as the 'brush' type by Deane (1902*c*) who also considered the taxa described from the deposit to be indicative of the Australian flora and did not suggest the existence of an outside element, as generally proposed by Ettingshausen (1888). Deane (1902*c*) describes a single incomplete leaf as the new species *Eucryphia gregorii* on the basis that it 'bears such striking resemblance to a pinna of *Eucryphia moorei* F.v.M., of New South Wales and Victoria, and to a leaf of *E. billardieri* Spach. {now *E. lucida* (Labill.) Baill.}, of Tasmania, that I feel justified in including it under the same genus'. The description and illustration by Deane (1902*c*) were available for this study as the original specimen could not be located.

Specimens examined (illustration and description only):

Eucryphia gregorii (Deane 1902*c*; Chapter 5)

2.5.28 Radoboj, Croatia, Europe

There is scant information on the age and stratigraphy of this fossiliferous deposit. Unger (1866) described numerous species of *Apocynophyllum, Myrsine, Symplocos,*

Diospyros, Gaultheria, Vaccinium, Acer, Clematis, Sapindus, Prunus, and *Quercus* from this deposit in Croatia. The deposit is Miocene in age (Sarmatian in Mai 1995).

Specimens examined (illustrations and descriptions only):

Ceratopetalum radobojanum (Chapter 3)

Cunonia europea (Chapter 6)

2.5.29 Regatta Point, western Tasmania

Three fossiliferous units that contain *Eucryphia* macrofossils occur at Regatta Point (see Jordan and Hill 1998). *Eucryphia microstoma* (Hill 1991*a*) has been described from the Early Eocene sediments at Regatta Point and is represented by a single specimen and numerous fragments of dispersed cuticle. These sediments also contain leaf fragments of a palm (*Nypa*, Pole and Macphail 1996), a cycad (*Bowenia*), *Gymnostoma* (Casuarinaceae) and several conifers (*Araucaria* species, Podocarpaceae and Cupressaceae).

The overlaying glacial outwash contains clay clasts of Early Pleistocene and Early-Middle Pleistocene age. Dispersed cuticle of an unknown *Eucryphia* species has been recorded from the Early-Middle Pleistocene clasts (Jordan *et al.* 1995) which also contain leaves with affinities to extant *Nothofagus, Athrotaxis, Orites revoluta, O. milliganii* and Epacridaceae.

The Early Pleistocene clasts are primarily aged on palynostratigraphy (Macphail *et al.* 1993*b*; Jordan and Hill 1994) and contain abundant mummified leaves and leaf fragments of *Eucryphia* that have been studied by Hill and Macphail (1985), Hill (1991*a*), Jordan (1992), Taylor (1993) and Taylor and Hill (1996). This Early Pleistocene flora has been extensively studied (e.g. Hill and Macphail 1985; Jordan 1992, 1995*a*, *b*, 1997, 1999; Macphail *et al.* 1993*b*) and included many extant Tasmanian rainforest species such as *Phyllocladus asplenifolius, Atherosperma moschatum, Nothofagus cunninghamii* (Hill and Macphail 1985), *Agastachys odorata, Cenarrhenes nitida, Telopea truncata, Lagarostrobos franklinii, Bauera rubioides, Orites revoluta* (Jordan 1995*a*) and *Microcachrys tetragona* (Jordan 1995*b*). Despite its recent age, several genera present in the deposit are now extinct in Tasmania, including *Dacrycarpus* (Jordan 1995*b*) and *Quintinia* (Macphail and Hill 1985; Jordan 1997).

Leaves and leaf fragments of *Eucryphia* were available for this study from all three fossiliferous units. Specimens from this locality have the prefix RPE (Early Eocene), RPA (Early-Middle Pleistocene), or RPU (Early Pleistocene) and are all housed in the School of Plant Science, University of Tasmania.

Specimens examined:

Bauera rubioides (Chapter 6)

RPA- no number assigned, dispersed cuticle

Eucryphia microstoma (Chapter 5)

RPE-028

Eucryphia sp. (Chapter 5)

RPA- no number assigned, dispersed cuticle

Eucryphia lucida leaves and leaf fragments (Chapter 5)

RPU-4640, 4650, 4657, 4666, 4670, 4673, 4678, 4679, 4683, 4687, 4686, 4691, 4693, 4702, 4718

Eucryphia milliganii ssp. *milliganii* leaves and leaf fragments (Chapter 5)

RPU-4639, 4653, 4655, 4660, 4680, 4689, 4684, 4698, 4707, 4711, 4715

2.5.30 Regency Formation, western Tasmania

The Regency formation occurs in western Tasmania. Fitzsimons *et al.* (1990) argued that it is Early-Middle Pleistocene in age but E. A. Colhoun (pers. com.) and Jordan and Hill (1994) considered that the age is more likely to be Middle Pleistocene based on sedimentological and palaeofloristic grounds. The flora was particularly diverse and included numerous extant Tasmanian rainforest species including *Athrotaxis selaginoides, Nothofagus cunninghamii, Phyllocladus aspleniifolius, Eucryphia milliganii, Cenarrhenes nitida* and *Lagarostrobos franklinii* (Fitzsimons *et al.* 1990; Jordan 1992) and at least one genus that is now extinct from Tasmania (*Quintinia*, Fitzsimons *et al.* 1990). Numerous macrofossils of *Eucryphia* have been extracted and studied by Fitzsimons *et al.* (1990) and Taylor (1993). These were re-examined during this study. Specimens are housed in the Department of Environmental Biology, University of Adelaide, and the School of Plant Science, University of Tasmania.

Specimens examined:

Eucryphia lucida leaves and leaf fragments (Chapter 5)

R- 20A, 20B, 20C, 20D, 20E

Eucryphia milliganii ssp. *milliganii* leaves and leaf fragments (Chapter 5)

R-10A, 10B, 10C, 20D, 80A, 80D

2.5.31 Stuart Creek (Eyre Formation), South Australia

The stratigraphy of the Stuart Creek locality has been described by Alley and Lindsay (1995) and Rowett (1997). The age of the leaf-bearing silcrete overlaying the Willalinchina sandstone is unclear but is most likely Miocene to Pliocene age (see Rowett 1997) and not ?Eocene as suggested by Alley and Lindsay (1995). The fossiliferous silcrete occurs as raised outcrops across a small area adjacent to Stuart Creek. Studies of the site using quadrats has identified at least 142 fossil leaf types, 50 fruit and seed types and two wood types (Rowett 1997). The silcrete preserves extensive leaf mats of *Eucalyptus*, including invaginations of seed capsules, leaves of *Brachychiton, Cochlospermum, Orites* and other broad-leaf angiosperms (Greenwood 1996; Rowett 1997). This association has been interpreted by Rowett (1997) to represent marginal monsoonal forest with well defined tropical and sclerophyllous components that probably persisted along the watercourses during dry periods.

A 'serrate-coarse' leaf type has been identified from the site that has been compared to Cunoniaceae (Rowett 1997), and in particular *Callicoma* (Greenwood *et al.* 1990). Numerous specimens of this serrate-margined leaf occur across several outcrops but has not been studied in detail so its affinities still remain unclear. A rock containing a single silcrete leaf impression (R364695) and a latex mould of an *in situ* leaf impression (Fossil Leaf Type No. 3) were examined in detail for this study. The latter specimen was not collected and remains *in situ* but was examined on site, in addition to other leaf impressions, during a field survey in 1998.

Specimens examined:

'Serrate-coarse' (Chapter 4)

R364695 (rock specimen), Fossil Leaf Type No. 3 (latex mould).

2.5.32 Vegetable Creek, New South Wales

Ettingshausen (1888) described a single leaf impression as *Callicoma primaeva* Ett. from Vegetable Creek (now Emmaville), New South Wales. The sediment age is ambiguous given Ettingshausen (1888) did not recognise the 'older' and 'newer' leads previously identified by David (1887) and provides no further locality identification other than 'Vegetable Creek'. In a review of Ettingshausen's New England Tertiary plant localities Pickett *et al.* (1990) suggest a minimum age of 30.4 ± 0.3 Ma (Middle Oligocene) based on the overlying basalt flow with an underlying Late Eocene palynoflora. The illustration and description by Ettingshausen (1888) were available for this study but the original specimen could not be located.

Specimens examined (illustration and description only):

Callicoma primaeva Ett. (Chapter 4)

2.5.33 West Dale, south-western Western Australia

The site stratigraphy and age of the West Dale locality have been discussed by Hill and Merrifield (1993). Macrofossils are Middle Eocene-Oligocene in age and are preserved as mineralised leaf tissue in a yellowish-brown siltstone and include Myrtaceae, *Agathis, Dacrycarpus, Gymnostoma, Nothofagus,* Lauraceae, *Banksieaephyllum* and a high diversity of other Proteaceae (Hill and Merrifield 1993). A single lanceolate leaf from West Dale was assigned to cf. *Callicoma* by Hill and Merrifield (1993) on leaf shape and the presence of a ridge of cutin around the stomatal pore but paired hair bases characteristic of extant *Callicoma serratifolia* were not located in their study. The prepared scanning electron microscope sample and photographs of the single specimen examined (WAM P.88.84A) by Hill and Merrifield (1993) were available for this study. The specimen is housed in the Western Australian Museum, Perth.

Specimens examined:

cf. *Callicoma* (Chapter 4)

WAM P.88.84A (holotype)

2.5.34 Wilson's Creek, central Tasmania

Fossils occur more or less in horizontally bedded siltstones and fine sandstones exposed for approximately 60 m along the bed and banks of Wilson's Creek at 146° 27' 25" E, 42° 19' 10" S, at about 460 m above sea level (Jordan and Hill 1998). The sediments are overlain and underlain by basalts. The sediments range from scarcely to moderately lithified, possibly due to heating from cooling lava. Other lenses of similar sandstones are exposed upstream, and apparently stratigraphically above the fossiliferous lens. The sediments are ?Latest Eocene-Early Oligocene based on palynostratigraphic evidence (M.K. Macphail pers. com. 1998). The presence of fossils of large leaved *Nothofagus*, a range of imbricate conifers and diverse extinct angiosperms supports this Early Tertiary age. The overlying and underlying basalts have not been dated. A single compression fossil of a *Eucryphia* leaf (WC-33) and an incomplete imparipinnate leaf of an indeterminate *Weinmannia* species (WC-236) were extracted from the sediments at this site.

Specimens examined:

Eucryphia mucronata (Chapter 5)

WC-33 (holotype)

Weinmannia indet. sp. (Chapter 6)

WC-236

2.5.35 Witherden's Tunnel, near Emmaville, New South Wales

This locality is another of Ettingshausen's Tertiary fossil sites. Ettingshausen (1888) describes the deposit as being of 'brown carbonaceous clay, under basalt'. A Late Eocene age has been placed on the deposit by Macphail (see Hill 1988) based on palynological data. Ettingshausen (1888) described two species of *Ceratopetalum, C. gilesii* and *C. macdonaldi* from the Witherden's Tunnel sediments. The illustrations and descriptions of both species were available for this study in addition to the original specimens examined by Ettingshausen (1888). The specimens are housed at the Australian National Museum in Sydney, Australia.

Specimens examined:

Ceratopetalum gilesii (Chapter 3)

F51162 (holotype)

Ceratopetalum macdonaldi (Chapter 3)
F58841 (holotype)

2.5.36 Yallourn Formation, Latrobe Valley, Victoria

This deposit overlays the Morwell Formation and has been dated as Early to Middle Miocene (Blackburn and Sluiter 1994; Sluiter *et al.* 1995), with sediments spanning the *Triporopollenites bellus* Zone of Stover and Partridge (1973). As for the Morwell Formation, families and genera represented as micro- or macrofossils within the deposit include Myrtaceae, *Nothofagus* (*Nothofagidites* pollen type), Casuarinaceae (*Gymnostoma*), Proteaceae (*Banksieaephyllum*, Cookson and Duigan 1950), Podocarpaceae (*Dacrycarpus* and *Podocarpus*), Saxifragaceae (*Quintinia*), Araucariaceae (*Araucaria* and *Agathis*), Elaeocarpaceae (*Elaeocarpus* endocarps, Christophel and Blackburn 1996) and Cunoniaceae (Blackburn and Sluiter 1994 and authors cited therein).

Blackburn (1985) described dispersed cuticle from this deposit as Cunoniaceae aff. *Geissois* sp. as it resembled extant *G. benthamii* from Australia. The taxon *Phyllites yallournensis*, described by Cookson and Duigan (1950) from this deposit, occurs in both the Yallourn and Morwell Formations (see also 2.5.20 Morwell Formation, Latrobe Valley, Victoria). It is represented by leaves and leaf fragments with well preserved cuticle. The descriptions and illustrations by Blackburn (1985) for both taxa were available for this study, in addition to the description and illustrations provided by Cookson and Duigan (1950) for *P. yallournensis*.

Specimens examined (illustrations and descriptions only):
Cunoniaceae aff. *Geissois* sp. dispersed cuticle (Chapter 6)
Taxon 28 (plate 26a in Blackburn 1985)
Phyllites yallournensis (Chapter 6)
N.M.V. 14777, 14778, 14779.

Chapter 3. Leaf and Fruit Macrofossils of *Ceratopetalum*

3.1 Introduction

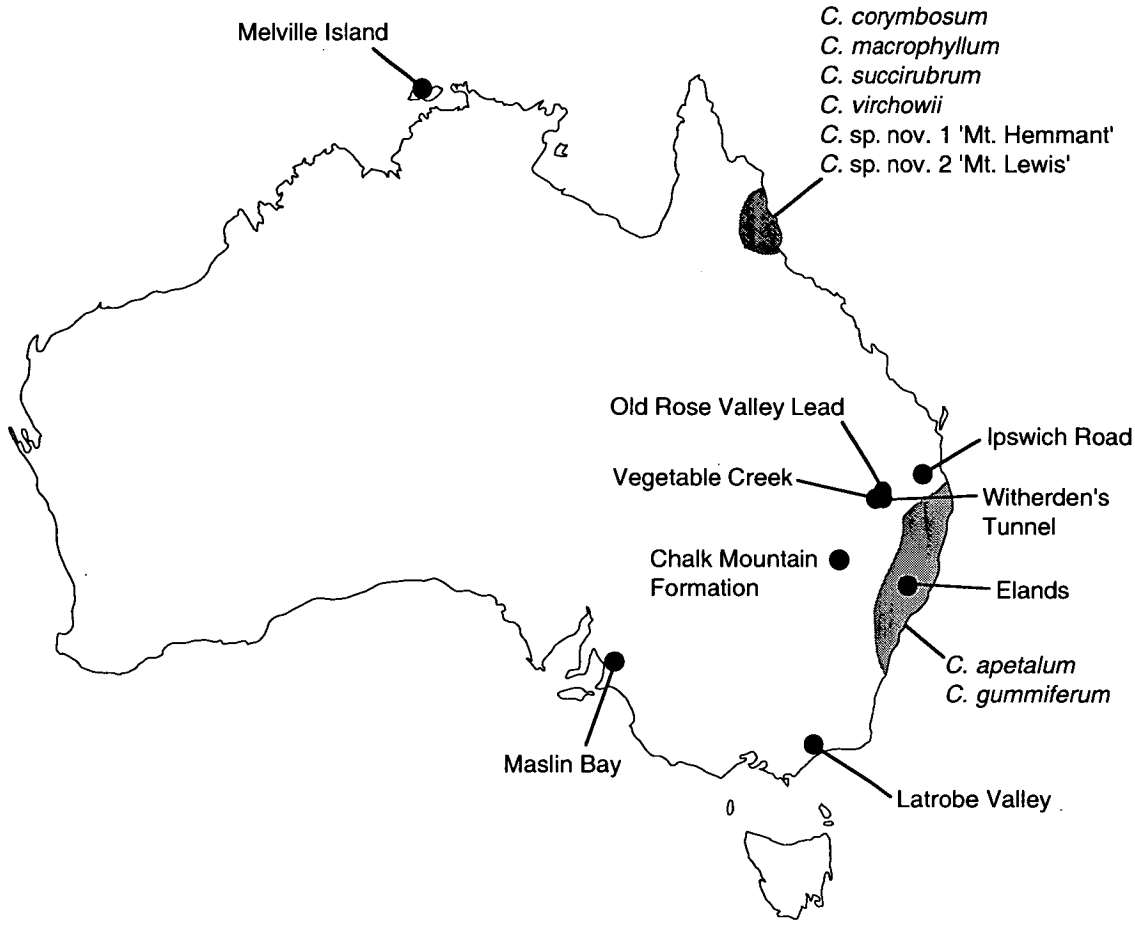
Ceratopetalum is a genus of six described (Hoogland 1960; Hoogland 1981) and at least two undescribed species (Hyland and Whiffin 1993; A. C. Rozefelds pers. com. 1999) that grow as trees to small shrubs predominantly on nutrient poor soils. The genus has a very disjunct distribution with two species, *C. gummiferum* and *C. apetalum*, distributed through rainforest and wet sclerophyll forests of south-eastern Australia, east of the Dividing Range (Fig. 3.1; Hoogland 1960; Boland *et al.* 1985; Floyd 1989). The remaining species, *C. corymbosum, C. macrophyllum, C. virchowii* and the two undescribed species are restricted to rainforest of generally higher altitude in north-eastern Australia (Fig. 3.1; Hyland and Whiffin 1993). *Ceratopetalum succirubrum* occurs in north-eastern Australia and in the rainforests of Papua New Guinea (Hoogland 1960).

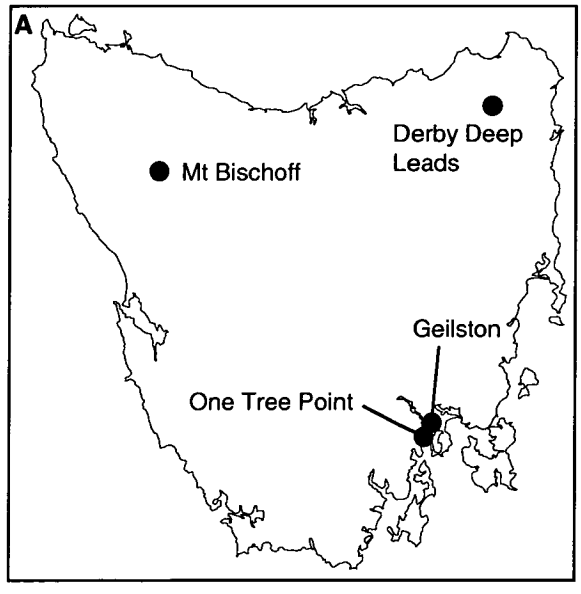
Morphologically, the genus has opposite decussately arranged, trifoliolate to unifoliolate leaves (Fig. 3.2.a-b). Interpetiolar stipules, characteristic of most Cunoniaceae, are present but variable in shape and size (see Fig. 3.2.a). In those species that are unifoliolate, the leaves are prominently articulated where the leaflet joins to the petiole, similar to that present in *Anodopetalum* (Barnes and Rozefelds 2000, Appendix 1).

Florally, the genus is characterised by possessing cymose inflorescences (Fig. 3.2.b), with bisexual, diplostemonous flowers that have valvate calyx aestivation, a semi-inferior bicarpellate ovary (Fig. 3.2.c-d). The fruit is dry and indehiscent with enlarged and woody sepals (Fig. 3.2.c; Hoogland 1960; Harden 1990*a*). Hufford and Dickison (1992) considered the sepal character an autapomorph for the genus. Petals are absent in all extant species except *C. gummiferum*, where bi- or tri-furcate petals occur in conjunction with a stamen, alternating with the corolla members (Fig. 3.2.a and c; Hoogland 1960; Harden 1990*a*).

Ceratopetalum is the most cited Cunoniaceae genus in the fossil record and is represented by both vegetative and floral organs (see Table 3.1). Historically, the name of an extant taxon was assigned to a leaf macrofossil on the basis that both superficially looked the same, or nearly so (e.g. Ettingshausen 1888). As extant

Fig. 3.1. Map of Australia showing the approximate Australian distribution of extant *Ceratopetalum* species (shaded). Fossil localities on mainland Australia, Tasmania (inset A) and New Zealand (inset B) where *Ceratopetalum* fossils have been reported are shown as circles. Geological ages and references for localities are listed in Table 3.1.


Melville Island
C. corymbosum
C. macrophyllum
C. succirubrum
C. virchowii
C. sp. nov. 1 'Mt. Hemmant'
C. sp. nov. 2 'Mt. Lewis'
Old Rose Valley Lead
Ipswich Road
Vegetable Creek
Witherden's Tunnel
Chalk Mountain Formation
Elands
C. apetalum
C. gummiferum
Maslin Bay
Latrobe Valley


A
Derby Deep Leads
Mt Bischoff
Geilston
One Tree Point

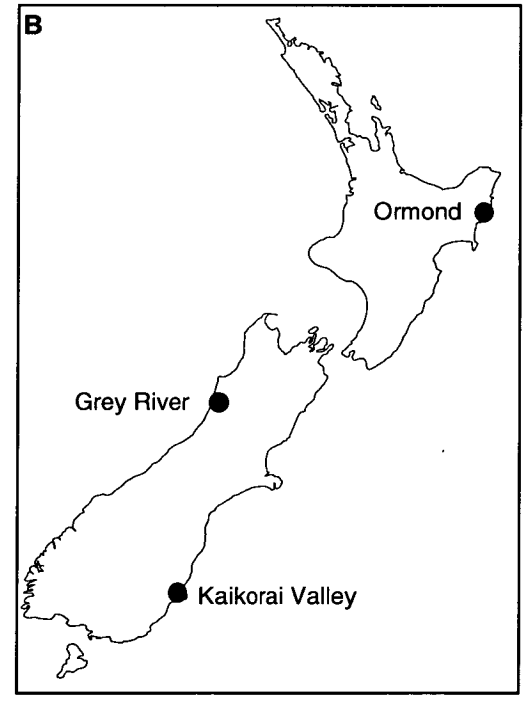

B
Ormond
Grey River
Kaikorai Valley

Fig. 3.2.a-d. Leaf and inflorescence morphology of extant *Ceratopetalum gummiferum.*

Fig. 3.2.a. Trifoliolate leaves are opposite and decussate in arrangement. The arrow indicates the position of the interpetiolar stipule. Note the diplostemonous flowers with tri-furcate petals. Scale bar = 20 mm.

Fig. 3.2.b. Cymose inflorescence architecture typical of other species in the genus. Note that flower maturation is not synchronous. Scale bar = 50 mm.

Fig. 3.2.c. Mature fruit showing persistent tri-furcate petals. Fruits turn bright red in this species prior to being shed from the tree. Scale bar = 20 mm.

Fig. 3.2.d. Cleared ovary and sepal bases showing three-trace vascularisation of sepals and fusion of laterals near the ovary before entering the receptacle (arrow). Veins originate from the pedicel below the ovary. Scale bar = 5 mm.

Figs 3.2.e-g. Line drawings of the sepal venation of extant *Ceratopetalum* species. Scale bar = 10 mm.

Fig. 3.2.e. *C. gummiferum.*
Fig. 3.2.f. *C. succirubrum.*
Fig. 3.2.g. *C. virchowii.*

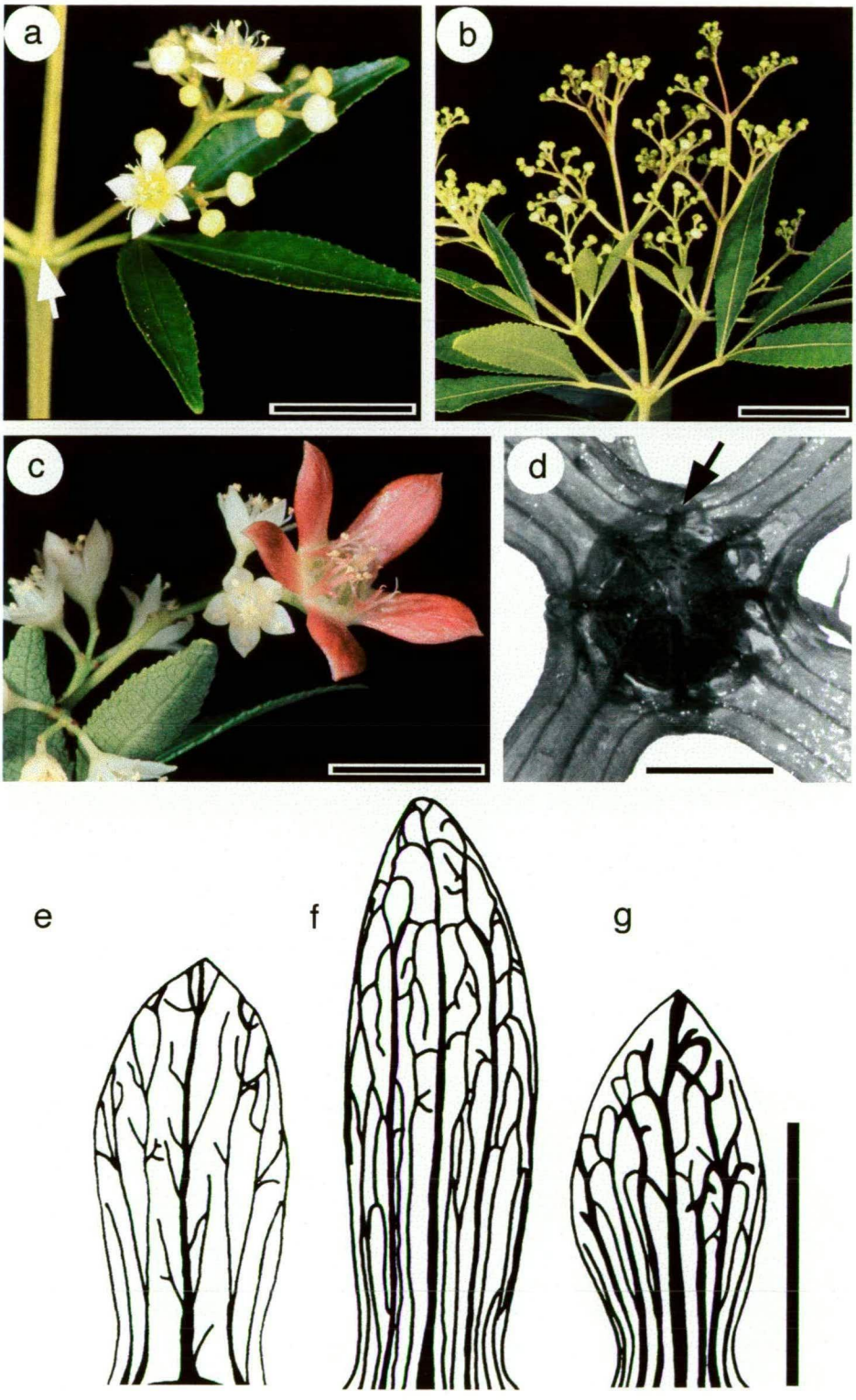

a
b
c
d
e
f
g

Table. 3.1. Macrofossil and microfossil records of *Ceratopetalum*

The Eocene-Recent age placed on the Melville Island deposit by White (1974) has been modified to Tertiary in age by Pole and Bowman (1996). This latter age was accepted for this study. Source: [A] Ettingshausen 1890; [B] Ettingshausen 1888; [C] Scott circa 1937; [D] Unger 1866; [E] Ettingshausen 1894; [F] White 1974; [G] Holmes and Holmes 1992; [H] Johnston 1885; [I] Luly *et al.* 1980; [J] Oliver 1936; [K] Oliver 1928.

Taxon	Fossil type	Geological age	Fossil locality
C. rivulare [A]	Leaf impression	Cretaceous	Grey River, New Zealand
C. praearbutoides [B]	Leaf impression	Upper Tertiary	One Tree Point, south-eastern Tasmania
C. woodii [B]	Leaf impressions	Upper Tertiary	Geilston, south-eastern Tasmania
C. clarkii [C]	Petrified wood	Early Tertiary	Derby Deep Leads, Tasmania
C. *radobojanum* [D]	Leaf ?impression	?Tertiary	Radobojanum, Croatia, Europe
C. americanum [B]	Leaf impression	Tertiary	North America
C. bilinicum [B]	Leaf	Tertiary	Europe
C. primigenium [E]	Leaf	Tertiary	Ipswich Road, Queensland
C. sp. cf. *C. macdonaldi* [F]	Leaf impressions	Tertiary	Melville Island, Northern Territory
C. gilesii [B]	Leaf compression	Late Eocene	Near Vegetable Creek, New South Wales
C. macdonaldi [B]	Leaf impression	Late Eocene	Near Vegetable Creek, New South Wales
C. wilkinsonii [G]	Fruit compression	Late Eocene-Early Oligocene	Old Rose Valley Lead, New South Wales
C. sp. [H]	Leaf ?compressions	Early to Late Oligocene	Mt. Bischoff, north-western Tasmania
C. 'complex' [I]	Pollen	Oligocene-Miocene	Latrobe Valley, Victoria
C. priscum [G]	Fruit compressions	Middle Miocene	Chalk Mountain Formation, New South Wales
C. kaikoraiense [J]	Leaf impression	Late Miocene	Kaikorai Valley, New Zealand
C. pacificum [K]	Leaf impression	Later Pliocene	Ormond, New Zealand

Ceratopetalum leaves are generally non-distinctive, bland and may appear to be superficially similar to some leaves of other families (e.g. *Elaeocarpus*, Elaeocarpaceae) it is not at all surprising that many leaf macrofossils were assigned to this genus. Therefore, the prolific erection of leaf fossil *Ceratopetalum* species is probably due to macrofossil misidentification rather than being indicative of an extensive fossil leaf record for the genus.

Leaf macrofossil species of *Ceratopetalum* have been described from Australian, New Zealand, and Northern Hemisphere Cainozoic sediments. Ettingshausen (1888, 1890, 1894), in his contribution to understanding Tertiary macrofloras, described several leaf fossils of *Ceratopetalum*, including for example, *C. woodii* from Upper Tertiary sediments at Risdon (Geilston in this study), Tasmania, which was compared with *C. bilinicum* leaves from European sediments; *C. praearbutoides* from Upper Tertiary leaf beds in the Derwent Valley (One Tree Point in this study), Tasmania, which was compared with *C. americanum* leaves from North American sediments; *C. macdonaldi* and *C. gilesii* from Late Eocene (Pickett *et al.* 1990) brown carbonaceous clays at Witherden's Tunnel, near Vegetable Creek, New South Wales. Oliver (1928; 1936) has described two fossil *Ceratopetalum* species from New Zealand, *C. pacificum* from Later Pliocene sediments at Ormond, and *C. kaikoraiense* Oliver from the Late Miocene Kaikorai Valley which he compared to both *C. pacificum* and *C. praearbutoides*. Flowers (fruits) of *Ceratopetalum* have been described by Holmes and Holmes (1992) from two Australian Cainozoic deposits.

A tentative record of *Ceratopetalum* pollen has been made from the Oligo-Miocene Yallourn and Morwell brown coal seams in the Latrobe Valley (Luly *et al.* 1980; Blackburn and Sluiter 1994) but most authors do not distinguish *Ceratopetalum* pollen from other dicolporate genera such as *Eucryphia* and *Anodopetalum* (e.g. Hill and Macphail 1983). This pollen record was not re-examined as it was beyond the scope of this study. Scott (circa 1937) identified wood from the Early Tertiary Derby deep leads, Tasmania, as *Ceratopetalum*.

The leaf macrofossil record of *Ceratopetalum* is reviewed, with some explanatory notes on the leaf morphology of the extant species. Two new fossil fruits from Australian Cainozoic sediments are described here as *Ceratopetalum* species and other fossil fruits/flowers previously assigned to this genus are reviewed. Features for identifying fossil *Ceratopetalum* leaves and fruits are discussed, in addition to the evolution of petally within the genus.

3.2 Materials and Methods

3.2.1 Leaf, Cuticle and Fruit Morphology of Extant Species

Fresh leaf material of all *Ceratopetalum* species, with the exception of *C. corymbosum*, was available from living plants housed at the School of Plant Science, University of Tasmania. Herbarium specimens supplemented the living collection to ensure the full geographic range of each species was sampled. Specimens examined are detailed in Appendix 3.

Extant and fossil specimens were photographed with a Canon EOS camera using transmitted or low angle light to highlight venation patterns. For well preserved fossils, whole specimens were examined with an Environmental Scanning Electron Microscope (ESEM) in wet mode at a pressure of 0.0 to 8.0 T.

3.2.2 Fossil Localities and Specimens

Detailed descriptions of each deposit and the macroflora they contain are provided in '2.5 Fossil Localities, Geological Ages and Specimens'. Fossil locations are shown in figure 3.1.

3.2.2.1 Witherden's Tunnel, near Emmaville, New South Wales

Ettingshausen (1888) described two species of *Ceratopetalum, C. gilesii* and *C. macdonaldi* from this Late Eocene (see Hill 1988) deposit. The illustrations and descriptions by Ettingshausen (1888) of both species were available for this study in addition to the original specimens.

3.2.2.2 Melville Island, Northern Territory

White (1974) describes specimen CPC 17128 from this deposit as *'Ceratopetalum'* with possible affinities to Ettingshausen's (1888) *C. macdonaldi* from Witherden's Tunnel. Pole and Bowman (1996) described Cupressaceae, Proteaceae (*Grevillea* and cf. *Dilobia*) and *Melaleuca* (Myrtaceae) from the sediment and redefined the age of the deposit as Tertiary. The illustrations provided by Pole and Bowman (1996) were available for this study.

3.2.2.3 One Tree Point, south-eastern Tasmania

This Early Tertiary deposit contains a leaf macrofossil described as *Ceratopetalum woodii* by Ettingshausen (1888). The original specimens examined by Ettingshausen (1888) could not be located but the description and illustration were available for this study.

3.2.2.4 Geilston, south-eastern Tasmania

This limestone deposit is at least Oligocene in age, or possibly older (Tedford *et al.* 1975). Ettingshausen (1888) described *Ceratopetalum woodii* from this locality, in addition to other taxa including *Araucaria, Cinnamomum* and *Fagus risdoniana.* The illustration and description of *C. woodii* by Ettingshausen (1888) was available for this study but the original specimen could not be located.

3.2.2.5 Ipswich Road, Queensland

Ettingshausen (1894) described species of *Fagus, Laurus, Cassia* and *Eucalyptus*, and a single species of *Ceratopetalum, C. primigenium*, from this Tertiary deposit. The illustration and description of *C. primigenium* by Ettingshausen (1894) were available for this study but the original specimens could not be located.

3.2.2.6 Grey River, New Zealand

Ettingshausen (1890) described *Ceratopetalum rivulare* from this Cretaceous deposit. The illustration and description of *C. rivulare* by Ettingshausen (1888) were available for this study but the original specimen could not be located.

3.2.2.7 Kaikorai Valley, New Zealand

The deposit is Late Miocene in age (Tremain 1988). The illustration and description of *C. kaikoraiense* by Oliver (1936) were used in this study as the original specimen could not be located.

3.2.2.8 Ormond (Waipoa Series), New Zealand

This deposit is Later Pliocene in age (Oliver 1928). The illustration and description of *C. pacificum* were used in this study (see Oliver 1928) as the original specimen could not be located.

3.2.2.9 Radoboj, Croatia, Europe

There is scant information on this locality and it is Miocene in age (Sarmatian in Mai 1995). The illustration and description by Unger (1866) of *C. radobojanum* were available for this study but the original specimen could not be located.

3.2.2.10 Mt Bischoff, north-western Tasmania

Microfossils indicate a Late Oligocene to Early Miocene age (Harris 1968 and 1973, cited in Jordan and Hill 1998), with a more recent and detailed palynological study supporting an Early to Late Oligocene age (S. M. Forsyth, pers. comm. to Jordan and Hill 1998). Some leaf forms in this deposit were considered by Ettingshausen to approach those in the fossil deposits at Breadalbane and One Tree Point (see description below), with particular reference to the genera *Ceratopetalum, Lomatia* and *Ficonium* (see Johnston 1885).

3.2.2.11 Elands, north-eastern New South Wales

Two organic fruits that can be assigned to extant *Ceratopetalum* have been extracted from this late Early-Late Miocene deposit (Hill and Whang 2000).

3.2.2.12 Maslin Bay, South Australia

Six specimens of fossil fruits all considered to represent a single *Ceratopetalum* species were examined from this Middle Eocene deposit (Alley 1987; Lindsay and Alley 1995).

3.2.2.13 Chalk Mountain Formation, New South Wales

Three *Ceratopetalum* fruits preserved in diatomite were described as the single species

C. priscum by Holmes and Holmes (1992). The illustration and description by Holmes and Holmes (1992) and photograph by White (1990) were available for this study.

3.2.2.14 Old Rose Valley Lead, near Emmaville, New South Wales

A single fruit from the Late Eocene-Early Oligocene (Picket *et al.* 1990) Vegetable Creek Deep Leads in northern New South Wales was extracted and identified as *Getonites wilkinsonii* Ett. by Ettingshausen (1888). Holmes and Holmes (1992) considered the specimen more representative of *Ceratopetalum* so re-assigned it to *C. wilkinsonii*. The illustrations and descriptions by Ettingshausen (1888) and Holmes and Holmes (1992) were available for this study.

3.2.2.15 Derby Deep Leads, north-eastern Tasmania

Fossil wood of *Ceratopetalum clarkii* Scott has been described from this Early Tertiary (?Miocene) locality (Scott ca. 1937). The description by Scott (ca. 1937) was available for this study.

3.3 Results

3.3.1 Extant *Ceratopetalum* Leaf Morphology

3.3.1.1 Leaf Morphology

Ceratopetalum species either possess unifoliolate or trifoliolate leaves (Fig. 3.3.a-g). The leaflets in a trifoliolate leaf are of similar shape and size, with the lateral leaflets usually distinguishable by their falcate base, although these are less obvious in *C. gummiferum* (Fig. 3.3.a) and *C. succirubrum* (Fig. 3.3.d). The terminal leaflet is either sessile (*C. gummiferum*, Fig. 3.3.a), shortly petiolate (*C.* sp. nov. 2 'Mt Hemmant', Fig. 3.3.c), or possesses an extended petiolule much longer than that in the lateral leaflets (e.g. *C.* sp. nov. 1 'Mt Lewis', Fig. 3.3.b). In some species, such as *C. succirubrum*, there is a phase change from unifoliolate to trifoliolate leaves upon plant maturity (Hyland and Whiffin 1993; R. W. Barnes pers. obs).

Ceratopetalum apetalum, C. corymbosum and *C. macrophyllum* have unifoliolate

Figs. 3.3.a-g. Leaf form in extant *Ceratopetalum* species.

Figs. 3.3.a-d. Species with trifoliolate leaves.

Fig. 3.3.a. *Ceratopetalum gummiferum.* The leaflets in this species are sessile. It is a common tree species in the wet forests of south-eastern and eastern Australia (Hoogland 1960). Scale bar = 20 mm.

Fig. 3.3.b. *Ceratopetalum* sp. nov. 1 (RFK/1501; 'Mt Lewis'). Note that the terminal leaflet is shortly petiolate. This species occurs in upland rainforest in a few locations in north-eastern Queensland (Hyland and Whiffin 1993; R. W. Barnes pers. obs.). It has been propagated at the University of Tasmania. Scale bar = 40 mm.

Fig. 3.3.c. *Ceratopetalum* sp. nov. 2 (RFK/3338; 'Mt Hemmant'). This species is only known from 2 locations in moderate altitude (600-700 m a.s.l.) well developed rainforest in north-eastern Queensland (Hyland and Whiffin 1993). It has been propagated at the University of Tasmania. Scale bar = 50 mm.

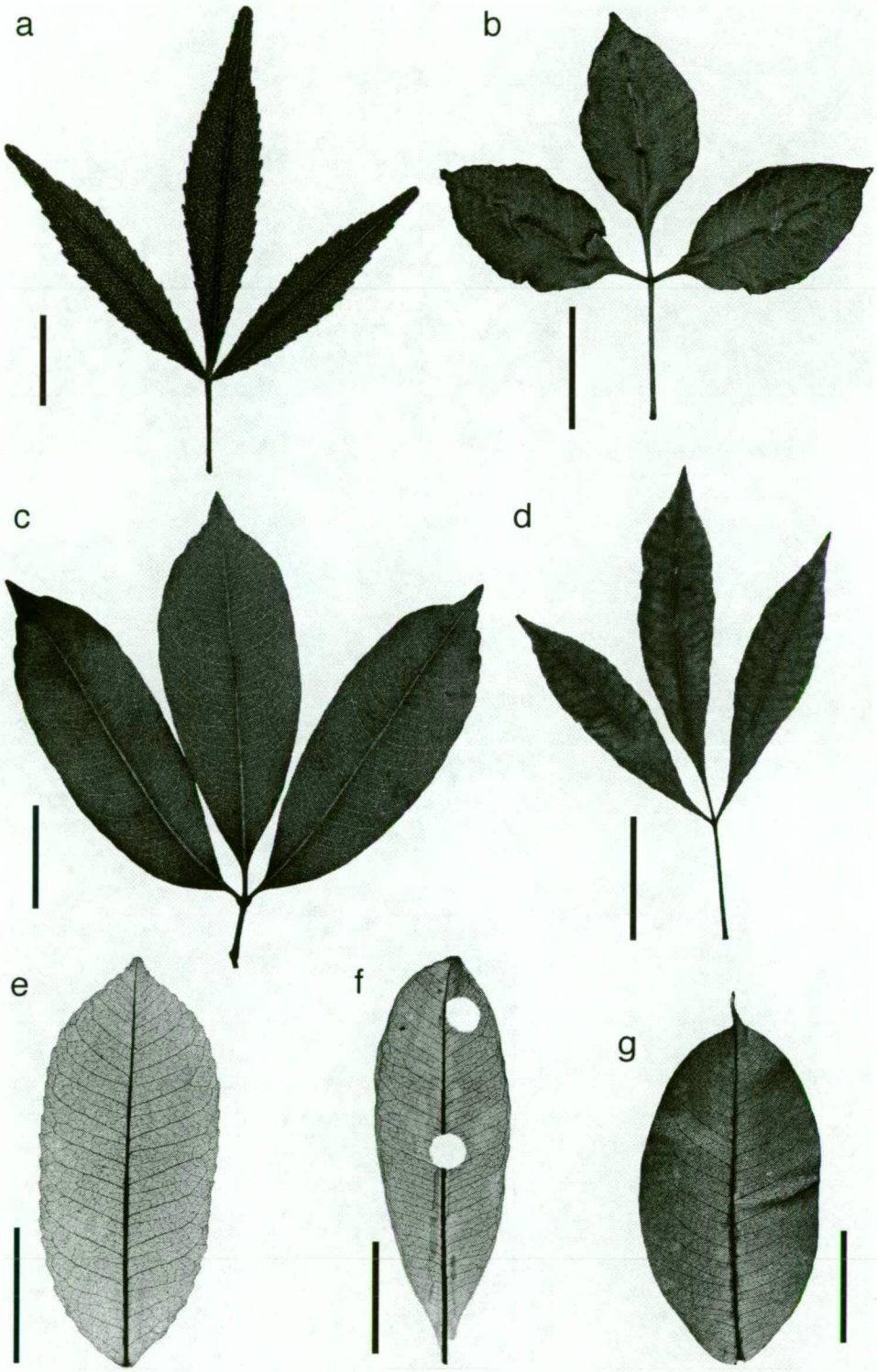
Fig. 3.3.d. *Ceratopetalum succirubrum.* Adult leaves (illustrated) are trifoliolate, or occasionally bifoliolate, while the juvenile leaves are unifoliolate with a prominent articulation between the leaflet and petiole. Scale bar = 50 mm.

Figs. 3.3.a-d. Species with unifoliolate leaves.

Fig. 3.3.e. *Ceratopetalum apetalum.* This species is a common tree species in coastal rainforests of south-eastern and eastern mainland Australia (Boland *et al.* 1985). Scale bar = 50 mm.

Fig. 3.3.f. *Ceratopetalum corymbosum.* This species is restricted to upland well developed rainforest in the Mt Spurgeon area of north-eastern Queensland (Hyland and Whiffin 1993). Scale bar = 30 mm.

Fig. 3.3.g. *Ceratopetalum macrophyllum.* The adult leaves have a slight cordate base and a very prominent drip tip. This species is endemic to the Noah Creek, Alexandra Creek and Roaring Meg Creek catchments in north-eastern Queensland (Hoogland 1981; Hyland and Whiffin 1993). Scale bar = 50 mm.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leaves (Fig. 3.3.e-g), where a single sessile leaflet is attached to the petiole. These leaves probably have their origins as trifoliolate leaves that have been reduced to a single leaflet, which has also been suggested to have occurred in *Anodopetalum* (Barnes and Rozefelds 2000, Appendix 1). The leaflet base is slightly cordate in *C. macrophyllum* and some specimens of *C. apetalum*, while in other species it is predominantly acute to cuneate. The leaflet apex in all species is obtuse, cuneate or attenuate with a drip tip present in most species, and is particularly prominent in *C.* sp. nov. 2 'Mt Hemmant' (Fig. 3.3.c) and *C. macrophyllum* (Fig. 3.3.g). Domatia are absent and the leaves are generally glabrous, or nearly so, with only a few trichomes occurring on the midrib, major veins and leaf margin.

The secondary venation pattern in all species is of the semicraspedodromous type (Fig. 3.4.a-e). Secondary veins vary in their angle of divergence from the midrib, with the most common condition being moderate (45-65°) to wide (65-80°), and is generally uniform over the length of the leaf. Tertiary venation is random reticulate with the presence of a composite intersecondary vein (Fig. 3.4.a-e), which is particularly prominent in *C. apetalum* (Fig. 3.4.a) and *C. corymbosum* (Fig. 3.4.c). This intersecondary vein can, in some cases, be nearly of equal size to the secondary veins. A vein originating from the secondary arch terminates at a glandular pubescent sinus. The tooth apices are vascularised by a vein originating from the sinus. All species have small spinose extensions on the tooth apices which tend to fall from the tooth as the leaf ages. These are particularly prominent in *C. gummiferum* and *C. apetalum.*

3.3.2.2 Cuticle Morphology

Leaves are hypostomatic with stomata arranged in areoles (Fig. 3.5.a-b). Subsidiary cell arrangement of the stomata is brachyparacytic (Fig. 3.5.c-d). Hydathodes have a brachyparacytic to stephanocytic subsidiary cell arrangement (Fig. 3.5.a-b) and occur on the major veins and within some areoles in association with the stomata (Fig. 3.5.a-b, e). The abaxial surface is generally smooth (Fig. 3.5.d-f) or the centre of each epidermal cell is slightly raised, forming small depressions where the epidermal cell walls occur (e.g. *C. corymbosum*, Fig. 3.5.g). This feature gives the appearance of the epidermal cells being slightly papillate, which also occurs in *Platylophus.* Abaxial epidermal cells are isodiametric to pentagonal in shape (Fig. 3.5.a-c). Epidermal cells on the major veins are elongate and linear (Fig. 3.5.b) or are square to isodiametric with non-sinuous cell walls (Fig. 3.5.a) but are less defined on minor veins and veinlets.

Figs 3.4.a-e. Venation patterns and tooth architecture in cleared leaf sections of extant *Ceratopetalum* species. The white arrow in each figure indicates the composite intersecondary vein. Scale bar in each figure = 10 mm.

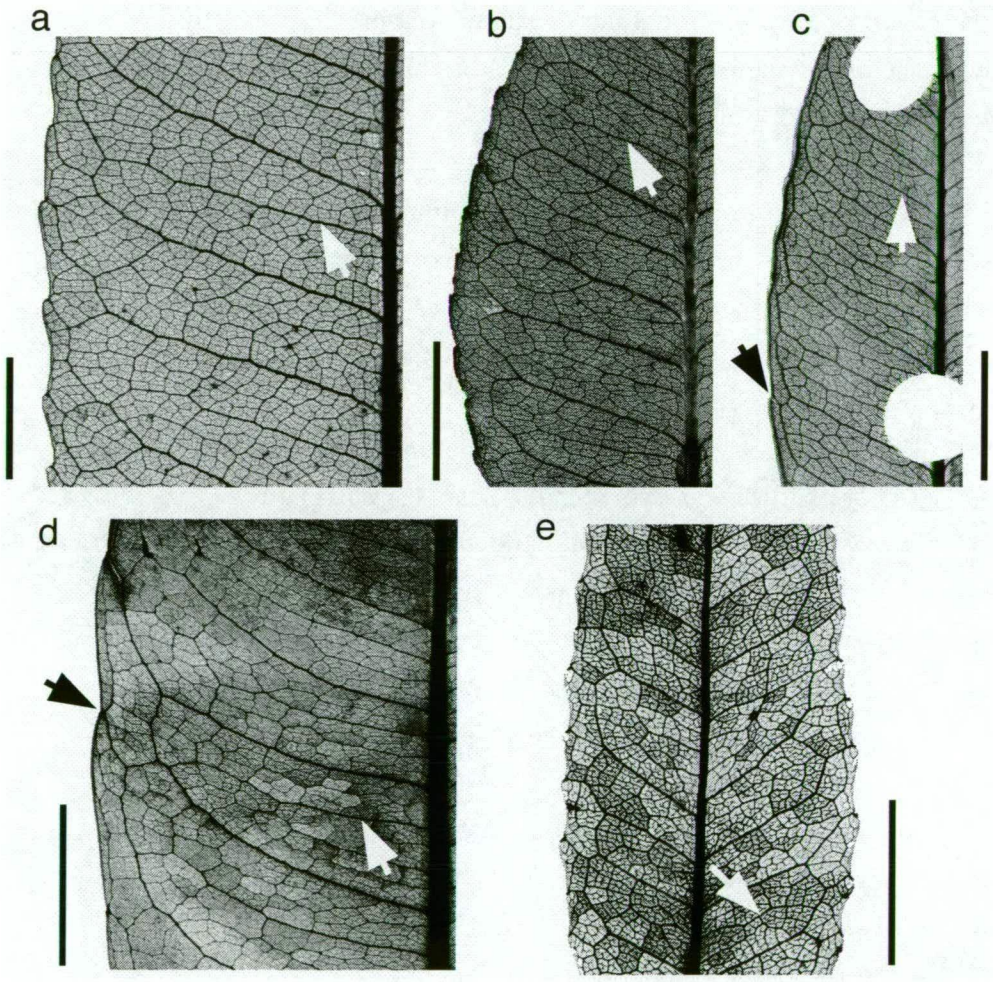
Fig. 3.4.a. *C. apetalum.* The secondary arches form well within the leaf margin. The fimbrial vein is well developed.

Fig. 3.4.b. *C.* sp. nov. 1 'Mt Lewis'.

Fig. 3.4.c. *C. corymbosum.* The leaf margin appears entire but there are small, reduced teeth along the upper portion of the leaf (black arrow). The secondary veins form arches immediately adjacent to the leaf margin and the fimbrial vein is well developed.

Fig. 3.4.d. *C.* sp. nov. 2 'Mt Hemmant'. The leaf margin appears entire but their are small reduced teeth along the leaf (black arrow). The tooth apices are glandular.

Fig. 3.4.e. *C. gummiferum.* Note the prominent marginal tooth apices which are glandular and possess a small spinose extension.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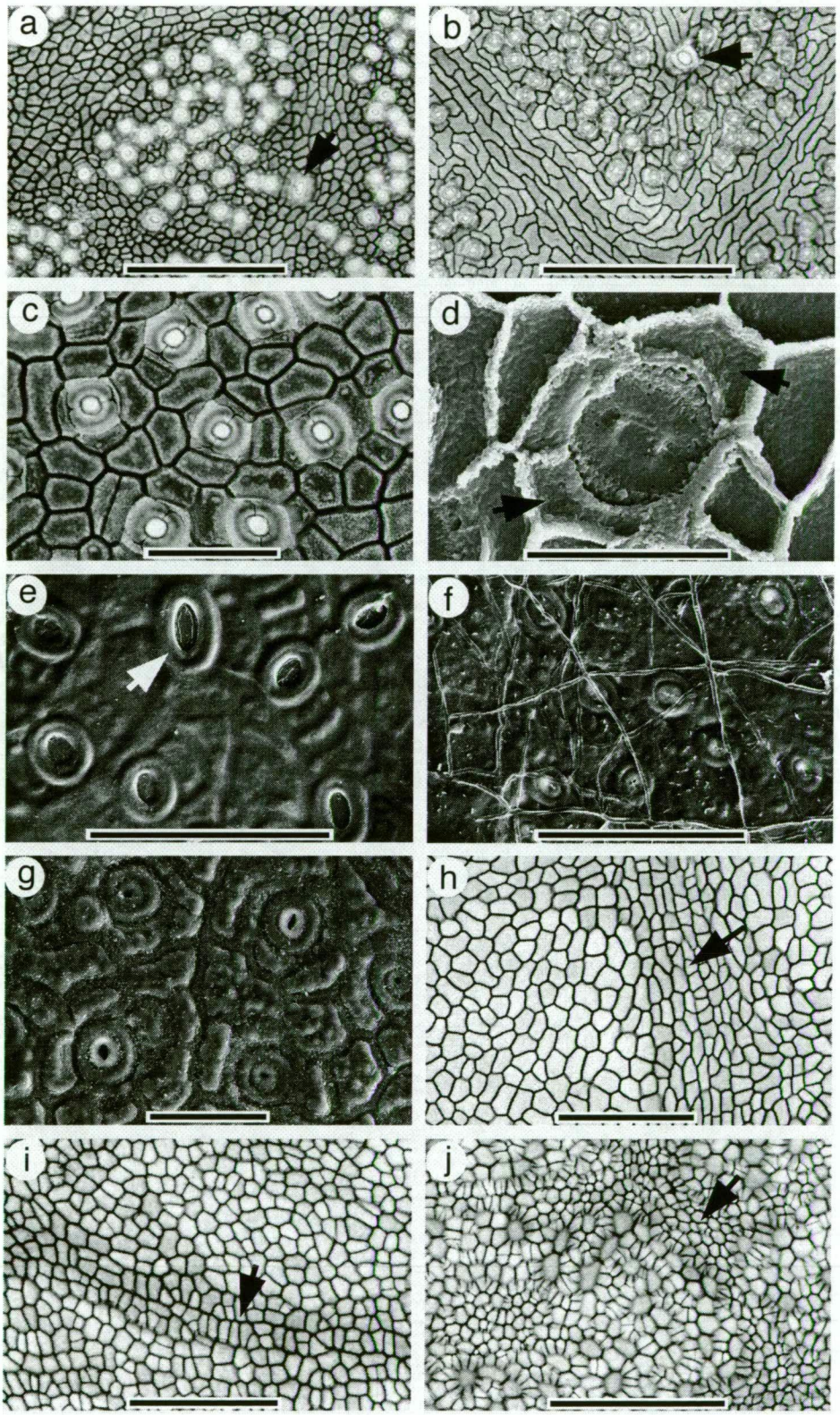
Figs 3.5.a-j. Cuticular features of selected extant *Ceratopetalum* species.

Figs 3.5.a-c. Light micrographs of the abaxial cuticle.
Fig. 3.5.a. *C. succirubrum.* Note the occurrence of stomata in areoles and the small, isodiametric shape of the venal cells. Hydathodes are present on the veins (arrow). Scale bar = 200 μm.
Fig. 3.5.b. *C. apetalum.* Stomata are not grouped into discrete areoles and the venal cells are more linear and slightly elongated. Hydathodes are present on the veins (arrow). Scale bar = 200 μm.
Fig. 3.5.c. *C. corymbosum.* Subsidiary cells have a brachyparacytic arrangement, and are recognised by the lighter areas of cuticle on the outer edge of each stoma. Scale bar = 50 μm.

Fig. 3.5.d. Scanning electron micrograph of the inner surface of a single stoma in *C. apetalum* showing the brachyparacytic arrangement of subsidiary cells (position of subsidiary cells indicated by arrows). Scale bar = 30 μm.

Figs 3.5.e-g. Scanning electron micrographs of the outer abaxial cuticle.
Fig. 3.5.e. *C. gummiferum.* Note the hydathode on the vein (arrow) and the absence of raised or papillate epidermal cells. Scale bar = 100 μm.
Fig. 3.5.f. *C. virchowii.* The epidermal cells are smooth and not raised. Note the presence of epicuticular wax strands. Scale bar = 100 μm.
Fig. 3.5.g. *C. corymbosum.* Note the small, but distinct, raised epidermal cells that are tending towards papillate. The depression between cells are the epidermal cell walls that are not raised. Scale bar = 50 μm.

Figs 3.5.h-j. Light micrographs of the adaxial cuticle. In each figure, the arrow indicates a vein. Scale bar for all = 200 μm.
Fig. 3.5.h. *C. apetalum.* Venal cells are well defined, linear and slightly elongated. Epidermal cells are isodiametric in shape.
Fig. 3.5.i. *C. succirubrum.* Venal cells are small and distinct from other epidermal cells.
Fig. 3.5.j. *C. corymbosum.* Note the lack of definition in the venal cells compared to other epidermal cells. The majority of epidermal cells are arranged in 'star'-like configurations where an enlarged central cell stellately surrounded by smaller epidermal cells, a feature present in other Cunoniaceae genera (e.g. *Codia,* Chapter 4).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The adaxial surface of all species is smooth and non-ornamented (Figs 3.5.h-j). Epidermal cells are isodiametric to pentagonal in shape and have straight walls. The adaxial epidermal cells in some species (e.g. *C. corymbosum*, Fig. 3.4.j) form star-like configurations where an enlarged central cell is radially surrounded by 5-9 smaller epidermal cells (Fig. 3.6.j), sometimes with corner thickenings. Venal cells are isodiametric, pentagonal or quadrangular in shape and are often smaller than other epidermal cells (see Fig. 3.4.h-j). In *C. succirubrum* (Fig. 3.5.i) and *C. corymbosum* (Fig. 3.5.j) the veins are less defined compared to those of *C. apetalum* (Fig. 3.5.h) and *C. gummiferum.*

Unicellular, non-glandular trichomes are rare on both surfaces, and are surrounded by 5-7 radially modified epidermal cells. Hair bases are of the 'peg' type described by Dilcher (1974) where the trichome cell forms part of the epidermis. There is only a small amount of thickening around the trichome bases.

3.3.2 Extant *Ceratopetalum* Fruit Morphology

Fruits of *Ceratopetalum* have 4-6 enlarged woody sepals radiating from the central disk (Fig. 3.2.c). Each calyx member is vascularised by 3 traces (Fig. 3.2.d-e) that originate from the receptacle and are not associated with the ovary (Fig. 3.2.d). Several species of *Ceratopetalum* (e.g. *C. succirubrum* and *C. virchowii*) were noted to be vascularised by additional (c. 7-9) smaller veins that originate from the receptacle or from the larger traces immediately after entering the calyx (Fig. 3.2.f-g). In all species, an intra-sepal marginal vein is formed by the fusion of laterals from adjacent sepals prior to entering the receptacle wall (Fig. 3.2.d). These veins remain unattached to the gynoecium which is vascularised by veins originating from the pedicel. The junction of the lateral veins coincides with a stamen in all species and a petal-stamen complex in *C. gummiferum* (Fig. 3.2.d). Sepals are constricted at the base but less so in some specimens of *C. succirubrum* (e.g. Fig. 3.2.f).

Petals are absent in all species except for *C. gummiferum*, where the petals are prominently tri-furcate and have a single vascular trace that enters at the base and alternate with the sepals (Fig. 3.2.c-d). The ovary is semi-inferior, bicarpellate and non-dehiscent (Fig. 3.2.c-d). Ovary size is variable, from 0.7 to 4.2 mm in diameter. Filaments are often persistent in mature fruit, with stamens twice as many as the sepals and occurring between and above each sepal. An annular nectary disk that is adnate to the ovary is present in all species and is often large and raised (e.g. *C. succirubrum*).

3.3.3 Fossil *Ceratopetalum* Leaves

In general, those fossils that lack good quality illustrations and/or detailed descriptions of leaf architecture are considered to be unverified or invalid as too little information is available to make any comment on their likely affinities. Illustrations and descriptions of *C. bilinicum* from Europe and *C. americanum* from North America (commented on by Ettingshausen 1888) could not be located for revision in this study.

3.3.3.1 Witherden's Tunnel, near Emmaville, New South Wales

Ceratopetalum macdonaldi was described from this locality by Ettingshausen (1888; Fig. 3.6.a-c), who indicated the secondary venation pattern was of the semicraspedodromous type (Fig. 3.6.b). However, the secondary venation pattern is clearly craspedodromous in the original specimen (Fig. 3.6.c). On this basis alone the fossil specimen is not a leaf of *Ceratopetalum*, and may instead represent *Nothofagus* although the formal assignment of the fossil to this taxon is premature and in need of further examination. The species *C. macdonaldi* is considered invalid.

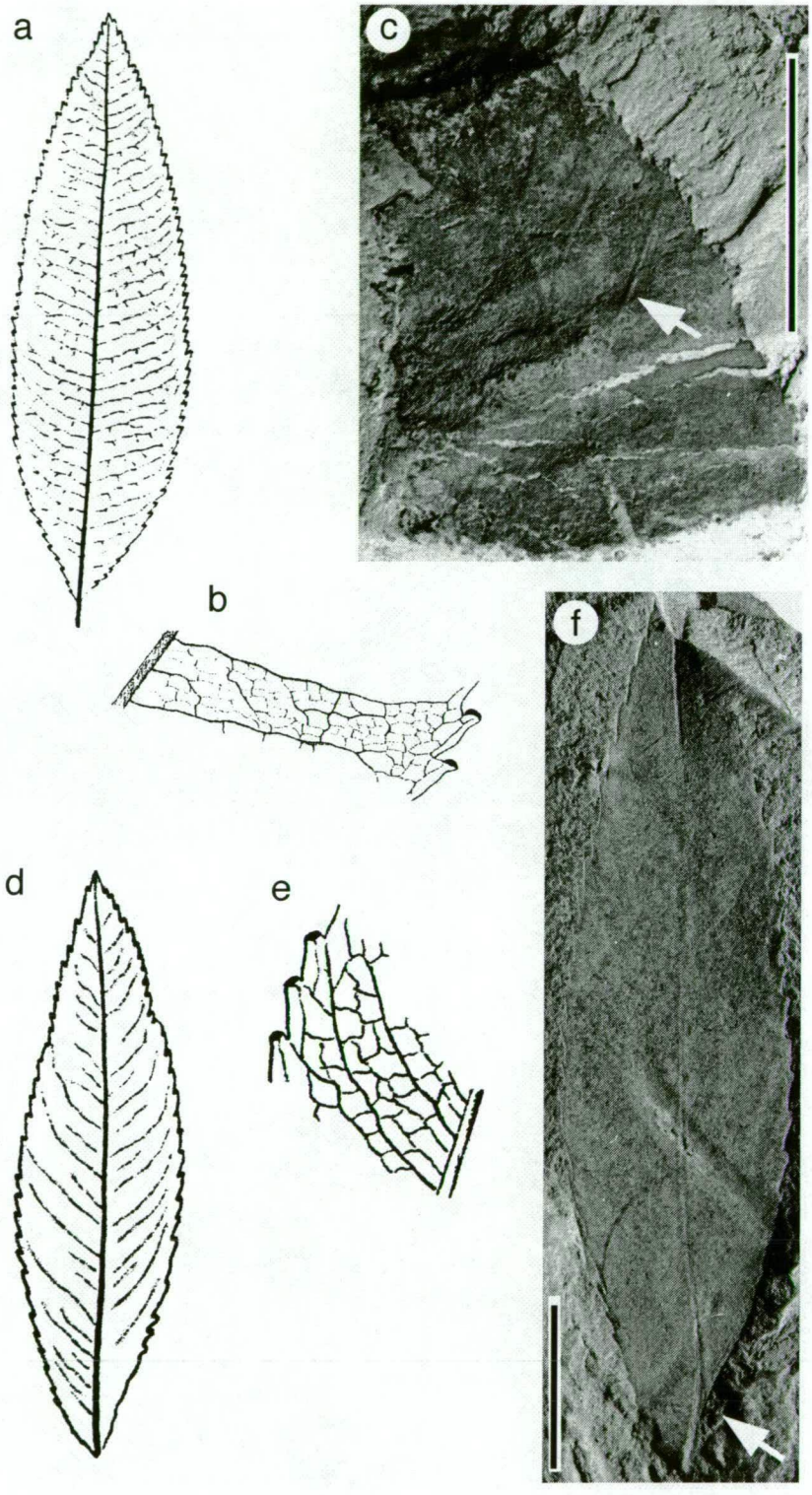
The impression fossil of *C. gilesii* is that of a leaflet based on the presence of a highly falcate base (Fig. 3.6.d-f), which was also suggested by Ettingshausen (1888). The leaflet has a serrate margin, with possibly glandular tooth apices (Fig. 3.6.e). The secondary venation pattern is semicraspedodromous and the tertiary veins are reticulate, which is in accordance with the findings of Ettingshausen (1888). However, very little extra data is preserved in the fossil specimen and it is therefore impossible to make any identification with confidence. Ettingshausen (1888) writes that 'It [the fossil specimen] corresponds exactly to *Ceratopetalum gummiferum* Smith, living in Australia from which it only differs, perhaps, by its secondary nerves being more curved along the borders...'. However, the specimen may equally represent a leaflet of another Cunoniaceae genus (e.g. *Platylophus*) or, and more likely, a genus of another family. This species will be excluded from further discussion until more data is available to assign it to *Ceratopetalum* with confidence.

Figs 3.6.a-c. *Ceratopetalum macdonaldi*. Line drawings are by Ettingshausen (1888).

Fig. 3.6.a. Line drawing showing venation of whole specimen.
Fig. 3.6.b. Line drawing of higher order venation.
Fig. 3.6.c. Macrofossil (specimen F. 58841). Arrow indicates a secondary vein that terminates at a glandular tooth apex (craspedodromous venation). Scale bar = 10 mm.

Figs 3.6.d-f. *Ceratopetalum gilesii*. Line drawings are by Ettingshausen (1888).

Fig. 3.6.d. Line drawing showing venation of whole specimen.
Fig. 3.6.e. Line drawing of higher order venation.
Fig. 3.6.f. Impression fossil (specimen F. 51162) with an asymmetrical leaf base (arrow). Scale bar = 10 mm.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3.3.3.2 Melville Island, Northern Territory

Pole and Bowman (1996) considered that one of the specimens (SB-950) they examined was the same fossil taxon that White (1974) described as Cunoniaceae (*Ceratopetalum* cf. *C. macdonaldi*, CPC-17128). This identification was considered invalid by Pole and Bowman (1996) on the basis that not enough detail was preserved and that there are no trifoliate Cunoniaceae in Queensland today that possess a terminal leaflet with an extensively elongated petiole (see illustrations by Williams *et al.* 1984). However, the two undescribed species of *Ceratopetalum* from north-eastern Queensland possess a terminal leaflet with an extended petiolule compared to that of the lateral leaflets (e.g. Fig. 3.3.b-c). Despite this, White's (1974) identification of the fossils as *Ceratopetalum* is still considered invalid until the original specimens are located and examined in more detail. Even in the event of the original specimen being located, it is unlikely that it preserves enough features to warrant formal identification.

3.3.3.3 One Tree Point, south-eastern Tasmania

For *C. praearbutoides*, no detail is provided in the description or illustration (Fig. 3.7.b) as to where the secondary veins terminate or loop, so the secondary venation pattern remains unknown. The fossil appears to be of a simple or unifoliate leaf, or possibly terminal leaflet of a compound leaf. Not enough detail is available in the illustration or description to warrant any identification to a modern genus so at this stage *C. praearbutoides* is considered to be an invalid species.

3.3.3.4 Geilston, south-eastern Tasmania

Ettingshausen (1888) compared *C. woodii* (Fig. 3.7.c) with *C. bilinicum* from European sediments and was considered to be trifoliate. However, this latter determination is not supported by his drawings as there is no organic connection shown between what he interpreted as the 'leaflets' (see Fig. 3.7.c). This lack of connection also implies that there is no reason to assume that these two leaves even represent the same taxon. The species *C. woodii* is considered invalid as there is too little information available in the illustration and description provided by Ettingshausen (1888).

Figs 3.7.a-h. Line drawings showing the venation of fossil *Ceratopetalum* leaf species. Most are historical records (e.g. Ettingshausen 1888, 1890, 1894) and the original specimens could not be located. Unless specified, no scale bars were placed on the original drawings. Scale bar when present = 10 mm.

Fig. 3.7.a. *C.* cf. *C. macdonaldi* from Melville Island, Northern Territory.

Fig. 3.7.b. *C. praearbutoides* from One Tree Point, Tasmania.

Fig. 3.7.c. *C. woodii* from Geilston, south-eastern Tasmania.

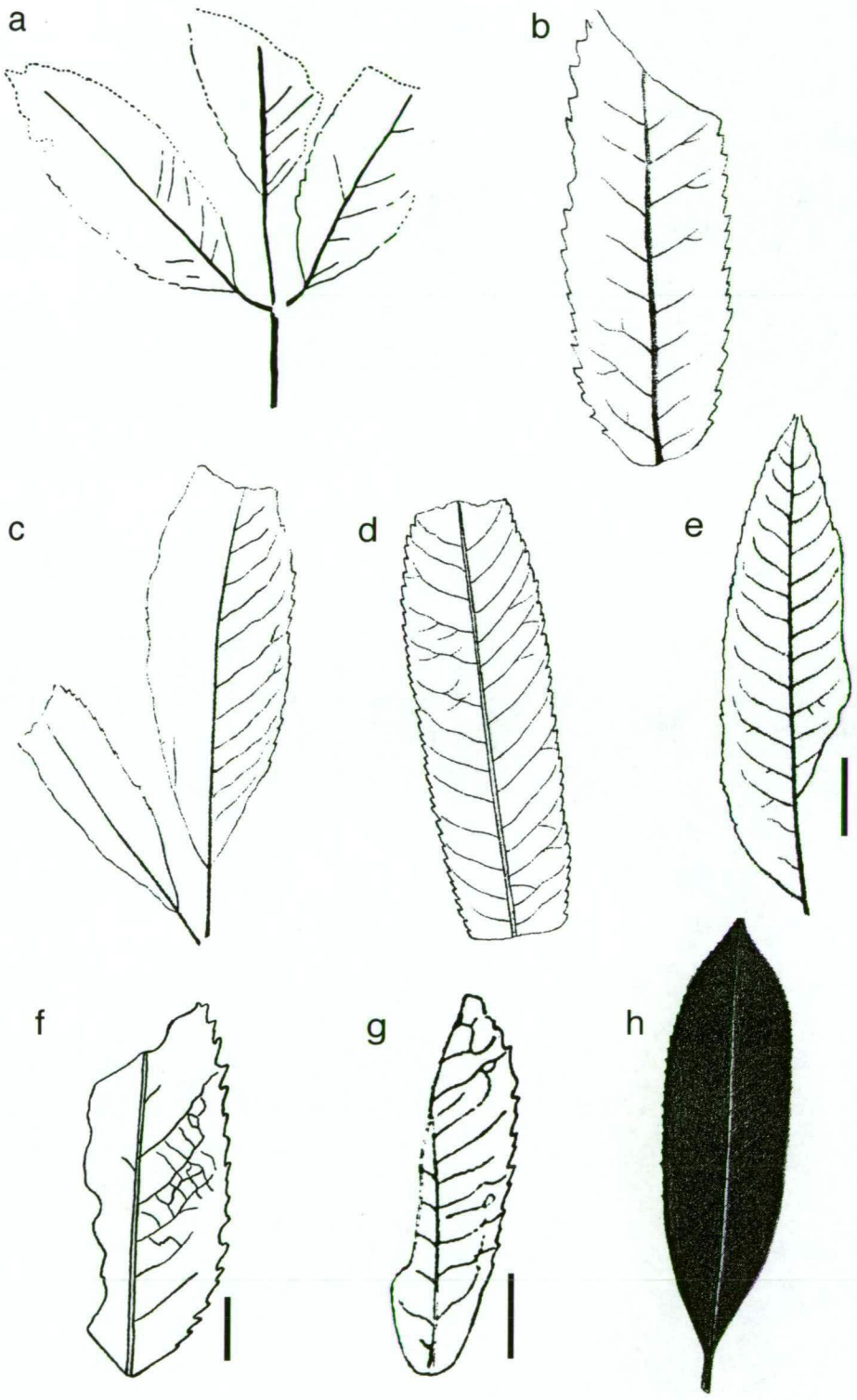
Fig. 3.7.d. *C. primigenium* from Ipswich Road, south-eastern Queensland.

Fig. 3.7.e. *C. rivulare* from the Grey River, New Zealand.

Fig. 3.7.f. *C. kaikoraiense* from the Kaikorai Valley, New Zealand.

Fig. 3.7.g. *C. pacificum* from Ormond, New Zealand.

Fig. 3.7.h. *C. radobojanum* from Radobojanum, Croatia, Europe.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3.3.3.5 Ipswich Road, Queensland

Ceratopetalum primigenium (Fig. 3.7.d) is described by Ettingshausen (1894) to be similar to *C. rivulare* from New Zealand (see below). The secondary venation pattern is said to be camptodromous in the species description by Ettingshausen (1894). This venation type occurs when the secondary veins do not terminate at the leaf margin (Hickey 1979), which is not the case for all extant *Ceratopetalum* species (see 3.3.1 Extant *Ceratopetalum* Leaf Morphology) and thus, the species *C. primigenium* is considered invalid.

3.3.3.6 Grey River, New Zealand

Ceratopetalum rivulare was compared to *C. macdonaldi* from Australia and *C. bilinicum* from North America by Ettingshausen (1890). The two specimens of *C. rivulare* (e.g. Fig. 3.7.e) do bear some resemblance to these two species, however they lack any features that can adequately identify it as *Ceratopetalum.* The species is considered invalid until the original specimens are located and examined in detail to provide enough data to warrant any identification.

3.3.3.7 Kaikorai Valley, New Zealand

Ceratopetalum kaikoraiense (Fig. 3.7.f) is represented by two incomplete leaf impressions (Oliver 1936), and consequently, very little data is preserved. The secondary veins are described by Oliver (1936) as not definitely looped which may indicate that the secondary venation pattern is craspedodromous, and then excludes any affinity to extant *Ceratopetalum.* In addition, the acute angle of divergence of the secondary veins from the midrib does not occur in any extant *Ceratopetalum* species. The species *C. kaikoraiense* is therefore considered to be invalid.

3.3.3.8 Ormond (Waipoa Series), New Zealand

Oliver (1928) provisionally placed a single fossil specimen from the Ormond deposit into the taxon *C. pacificum* (Fig. 3.7.g) as he considered it to be '...not unlike the Recent and Tertiary *Ceratopetalum* of Australia...', most presumably those described by Ettingshausen (1888, 1890). The acute angle of divergence of the secondary veins from the midrib illustrated to occur in the fossil is not present in any extant *Ceratopetalum* species. There is too little information provided by Oliver (1928) on

the venation type in this fossil, and the data that can be obtained from the drawing (Fig. 3.7.g) does not support any affinity to extant *Ceratopetalum*. Consequently, *C. pacificum* is considered invalid.

3.3.3.9 Radoboj, Croatia, Europe

There is not enough data provided in the illustration (Fig. 3.7.h) and description of *C. radobojanum* by Unger (1866) to assign the fossil specimen to any extant genus with any level of confidence. Indeed, the fossil specimen appears to be indistinguishable from those specimens that Unger (1866) assigned to the species *Samyda europea* Ung. On this, and the current distribution of the extant genus (Fig. 3.1), the species *C. radobojanum* is considered here to be misinterpreted as Cunoniaceae.

3.3.3.10 Mt Bischoff, north-western Tasmania

No specimens, descriptions or illustrations of *Ceratopetalum* leaves have been located for this site. Therefore, the occurrence of *Ceratopetalum* in this deposit, as suggested by Johnston (1885), is rejected until such time that the original specimens are examined or the site revisited to collect more material for examination.

3.3.4 Fossil *Ceratopetalum* Fruits

3.3.4.1 Elands, north-eastern New South Wales

The fossil fruits are assigned to *Ceratopetalum* based on the presence of enlarged sepals (Fig. 3.8.a-d), a semi-inferior bicarpellate ovary (Fig. 3.8.e), anthers occurring between and above sepals (Fig. 3.8.f) and an intra-sepal marginal vein formed by the fusion of laterals from adjacent sepals prior to entering the receptacle wall (Fig. 3.8.f-g). The sepals in both macrofossils are vascularised by three traces; a prominent central bundle with two adjacent bundles that anastomose with the central bundle in the upper portion of each sepal (Fig. 3.8.g). Smaller veins from the receptacle are absent. Towards the ovary, adjacent bundles anastomose and enter the receptacle wall which also provides a vascular trace to each stamen (Fig. 3.8.e-f).

The fossil fruits described here are similar to *C. gummiferum* in sepal venation as both have three prominent veins that originate from the receptacle wall (Fig. 3.2.d-e).

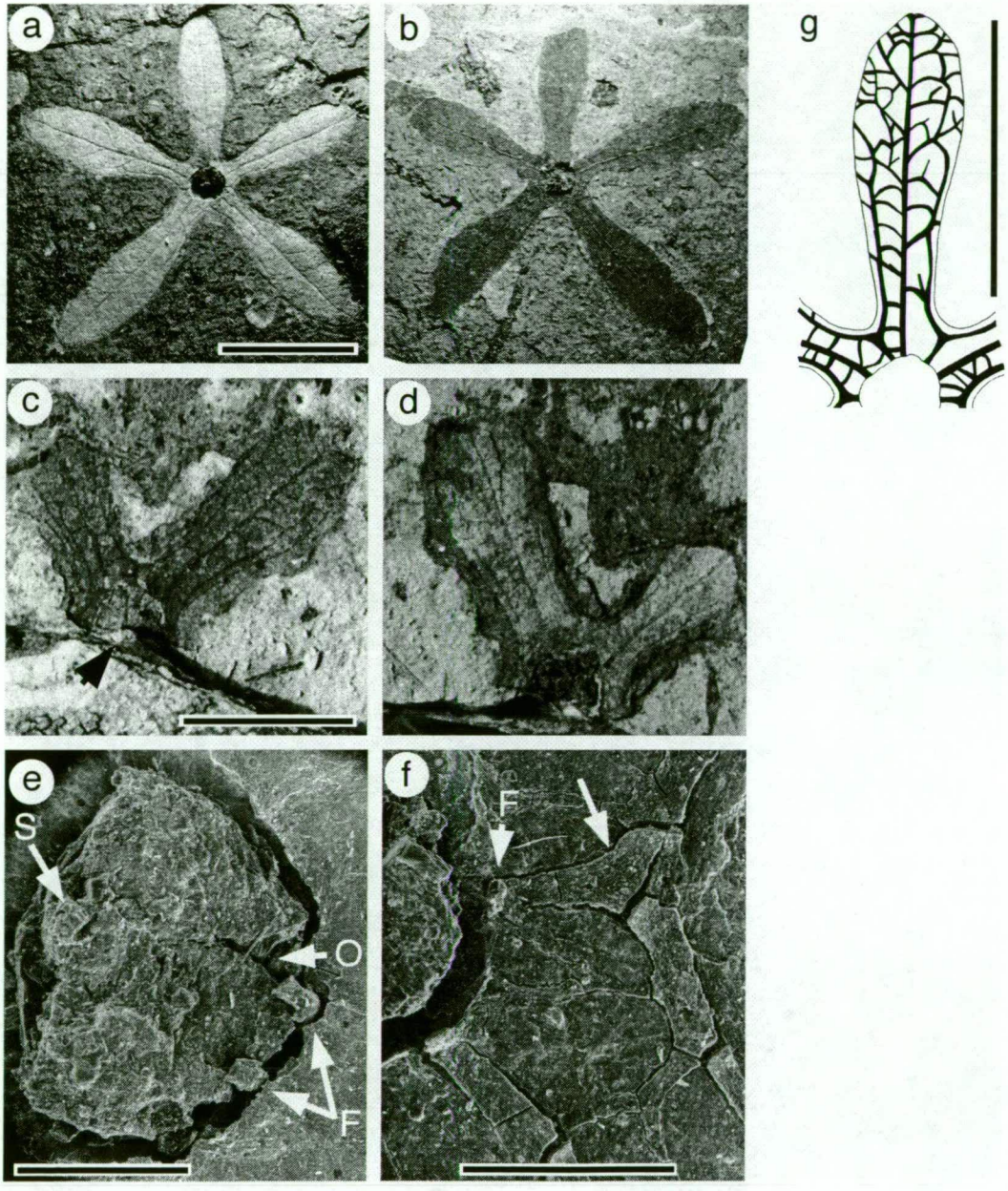
Figs 3.8.a-g. *Ceratopetalum westermannii* from Elands, north-eastern New South Wales.

Figs 3.8.a, b. Five-partite fruit (holotype; ELD-20). Scale bar for both = 10 mm.
Fig. 3.8.a. Impression counterpart.
Fig. 3.8.b. Organic counterpart with central ovary well preserved.

Figs. 3.8.c, d. Fruit (ELD-21) with 2 sepals preserved. Scale bar for both = 5 mm.
Fig. 3.8.c. Organic counterpart showing sepal venation and central receptacle (arrow).
Fig. 3.8.d. Impression counterpart.

Figs 3.8.e, f. Scanning electron micrographs of the holotype (ELD-20) ovary.
Fig. 3.8.e. Whole ovary showing the remains of anther filaments (F) surrounding the ovary. The split in the bicarpellate ovary (O) and the remains of an apical stigma and style (S) are both preserved. Scale bar = 500 μm.
Fig. 3.8.f. Lateral sepal veins fuse to form an intra-sepal vein (large arrow) prior to entering the receptacle wall. An anther filament vein (F) is also preserved. Scale bar = 500 μm.

Fig. 3.8.g. Line drawing showing the venation of a single sepal in the holotype (ELD-20). Scale bar = 10 mm.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S
O
F
f
F
g

However, *C. gummiferum* differs from the fossils as it is petalous and has multiple smaller veins towards the sepal base that originate from the laterals (Fig. 3.2.e). In addition, the lateral veins only weakly anastomose with the central bundle while in both fossils the laterals anastomose in the upper calyx to form a well defined, reticulate network of loops, unique in the genus (Fig. 3.8.g). This feature combined with the small size and shape of the calyces, the lack of multiple calyx veins originating from near the receptacle, strongly perpendicular cross veinlets and the absence of petals distinguishes it from any living or fossil species so it is here assigned to a new species, *C. westermannii.*

3.3.4.2 Maslin Bay, South Australia

The fossil fruits are typical of *Ceratopetalum* based on the presence of enlarged sepals radiating from the central disk, three-trace sepal vascularisation and a semi-inferior ovary (Fig. 3.9.e-f). The ovary is bicarpellate (Fig. 3.9.f) in one specimen but is poorly preserved in the remainder. Although fossil fruit size is variable, ranging from 8 to 14 mm in diameter, and the number of sepals varies from 5 to 6, the pattern of sepal vascularisation is consistent between all specimens. On this basis, all specimens are considered to represent a single taxon that was variable for both these attributes, similar to the level of variability present in most extant species (e.g. *C. succirubrum*).

Three prominent veins vascularise each sepal and only weakly anastomose in the distal part of the sepal (Fig. 3.9.b and d). This venation pattern and the presence of non-constricted sepal bases separates the fossil fruits from all extant species. The sepal venation pattern is similar to that of the fossil species *C. priscum* but differs from it by being apetalous. Therefore, the fruits are here assigned to a new species, *C. maslinensis.*

3.3.4.3 Chalk Mountain Formation, New South Wales

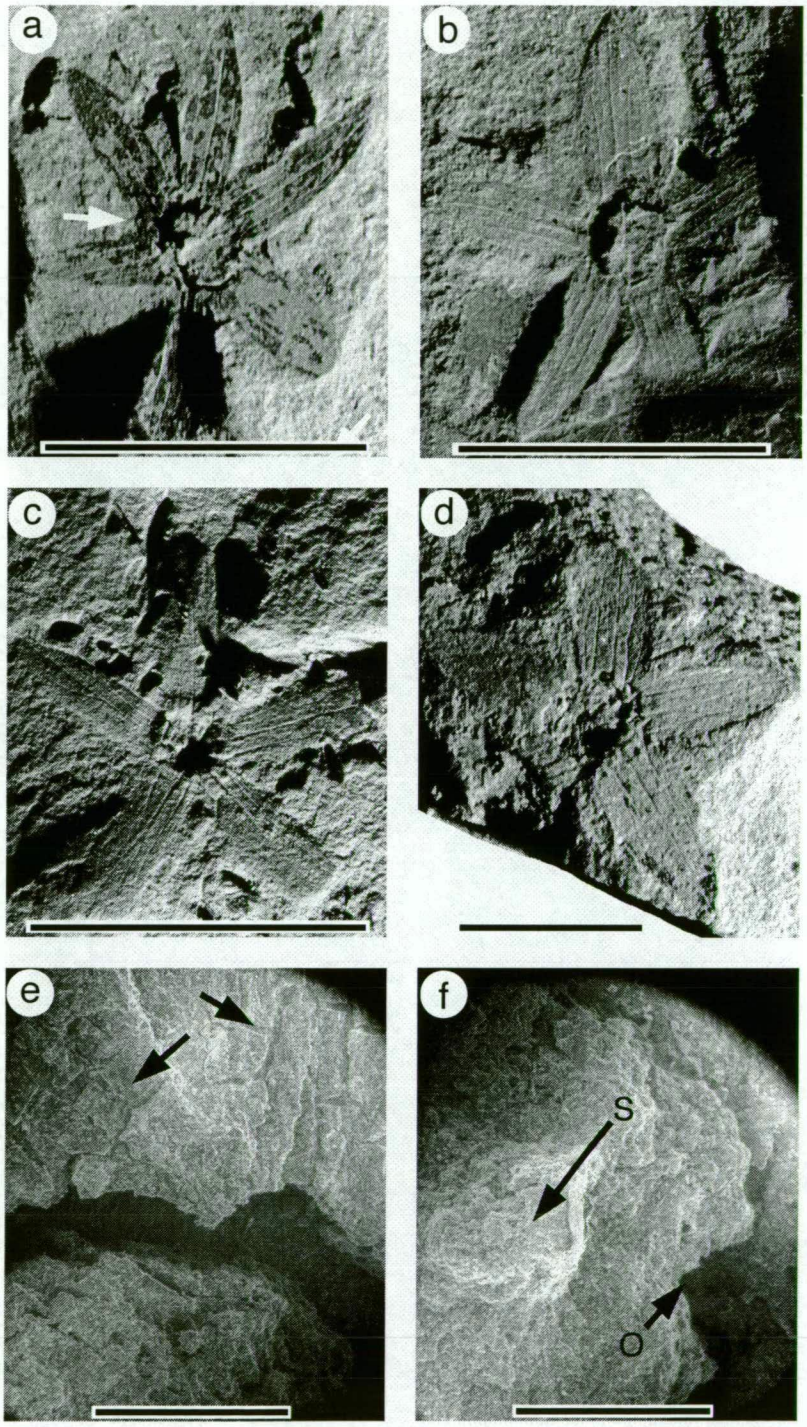
Holmes and Holmes (1992) indicated an affinity of *C. priscum* to extant *C. gummiferum* (Fig. 3.10.a cf. Fig. 3.2.c) based on the presence of ?tri-furcate petals. Prominent three-trace sepal venation with few cross veinlets that frequently terminate blindly also support an affinity to *C. gummiferum* but it is distinct from it due to the absence of basally constricted calyces and the presence of straight vascular traces the length of the sepal (Fig. 3.10.a cf. Fig. 3.2.e). The determination of Holmes and Holmes (1992) that this fossil (specimen MMF25501) represents a distinct species is

Figs 3.9.a-f. *Ceratopetalum maslinensis* from Maslin Bay, South Australia.

Fig. 3.9.a. Coalified compression of six-partite fruit (holotype; S-6000). Note the absence of petals (arrow) and well preserved ovary (centre). Scale bar = 10 mm.

Fig. 3.9.b-d. Impressions of a five-partite fruits.
Fig. 3.9.b. S-840. Scale bar = 10 mm.
Fig. 3.9.c. S-6002. Scale bar = 10 mm.
Fig. 3.9.d. S-1786. Scale bar = 5 mm.

Figs 3.9.e-f. Scanning electron micrographs of the ovary of specimen S-6000.
Fig. 3.9.e. Semi-inferior ovary (base) showing a lack of attachment to the sepals. The arrows indicate the base of two of the sepals that radiate from the central disk. Scale bar = 500 μm.
Fig. 3.9.f. Bi-carpellate ovary showing the split between carpels (O) and the remnants of apical styles (S). Anther filaments are not preserved. Scale bar = 500 μm.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S
O

supported. Two paratypes are also listed by Holmes and Holmes (1992) as being apetalous which may suggest another species co-occurred with *C. priscum.* However, the specimen illustrated by White (1990; p. 197), which is one of these paratypes, has remnant single trace structures between the sepals which are probably incomplete petals similar to those in the holotype.

3.3.4.4 Old Rose Valley Lead, near Emmaville, New South Wales

The fruit has five enlarged woody sepals stellately arranged around a poorly preserved central disk and a semi-inferior ovary (Fig. 3.10.b). The diagnosis of *C. wilkinsonii* in its current form (Ettingshausen 1888; Holmes and Holmes 1992) is not considered unique and has inaccurate interpretations of several structures. Holmes and Holmes (1992) described the fossil as having an unusually large ovary for the genus (6.5 mm in diameter), but this measurement included the remains of a large raised nectary (present in extant species) and the ovary is, in fact, well within the range of other species at 3.6 mm in diameter. During preservation the nectary was compressed onto the sepals which can be seen by the persistence of clear sepal venation below what Holmes and Holmes (1992) considered to be the ovary.

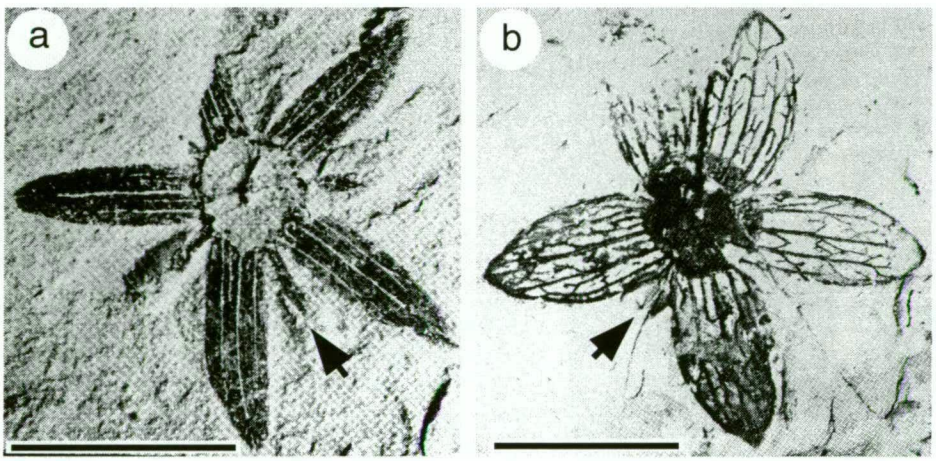
The remains of structures between two sepals were considered to be stamens by Ettingshausen (1888) and possible petals by Holmes and Holmes (1992). The structures are vascularised by a single trace which trifurcates into 3 separate lobes, similar to petals in *C. gummiferum.* This structure is interpreted here as a solitary, intra-sepal, tri-furcate petal which distinguishes the fruit from all extant species except for *C. gummiferum.* It is also distinct from *C. gummiferum* as it has broadly ovate, multiple (c. 5) veined calyces (Fig. 3.10.b cf Fig. 3.2.e). The incomplete reticulum described by Holmes and Holmes (1992) is the result of incomplete fusion of lateral traces, a feature common in most extant species (e.g. Fig. 3.2.e-g). The recognition of petals in the fossil combined with the sepal venation pattern, shape and constricted bases separates the fruit from all extant and fossil species. An emended diagnosis for *C. wilkinsonii* is presented here which includes the presence of petals.

3.3.5 Fossil *Ceratopetalum* Wood

The fossil wood described as *Ceratopetalum clarkii* by Scott (circa 1937) is lacking any diagnostic features to be assigned to this genus. The record is considered dubious, and most probably invalid.

Fig. 3.10.a. *Ceratopetalum priscum* (holotype; MMF25501) from the Chalk Mountain Formation. Arrow indicates a tri-furcate petal. Scale bar = 10 mm.

Fig. 3. 10.b. *Ceratopetalum wilkinsonii* (holotype; MMF8812) from the Old Rose Valley Lead (near Vegetable Creek). Arrow indicates a single tri-furcate petal. Scale bar = 10 mm.


a
b

3.4 Systematics

The systematics of all the below mentioned fossils are detailed in Barnes and Hill (1999*a*; Appendix 1).

Family: Cunoniaceae R.Br.

Ceratopetalum Sm.

Ceratopetalum westermannii R.W.Barnes & R.S.Hill, sp. nov. (Fig. 3.8.a-g).

Diagnosis: Fruit five-partite, sepals narrow obovate, apices round, bases contracted. Three vascular traces only per sepal that anastomose with central bundle at half length of sepal. Reticulate venation in upper sepal. Petals absent.

Holotype: ELD-20 and counterpart (stored in the School of Plant Science, University of Tasmania).

Type locality

Sediments of late Early-Late Miocene age at Elands, about 50 km NNW of Taree, northern New South Wales.

Specimens examined

ELD-21 and counterpart (retained by Hans Westermann).

Etymology

Named after Hans Westermann who discovered the deposit in 1995.

Description: The fruit is c. 19 mm in diameter with enlarged, prominently three veined sepals that have small apically directed cross veinlets. Sepals are entire, 6-9 mm in length and 1.8-2.2 mm wide, obovate and constricted at the base with a rounded apex. Each sepal is vascularised by a central bundle from the receptacle wall with lateral veins from adjacent sepals anastomosing to form an intra-sepal marginal vein prior to entering the receptacle wall. Two prominent lateral veins persist for half the length of each sepal and then fuse with the central bundle. In the upper sepal there is a network of reticulate veins which anastomose to adjacent veins or terminate at the sepal margin. Petals are absent, and there are 10 stamens (based on anther filaments preserved between and above each sepal). The ovary is bicarpellate, half-inferior, c. 1.0-1.2 mm

in diameter and non-dehiscent. A nectary surrounding the ovary is absent or very poorly preserved.

Ceratopetalum maslinensis R.W.Barnes & R.S.Hill, sp. nov. (Fig. 3.9.a-f).

Diagnosis: Sepals narrow oblong, apices acute-obtuse, not contracted at the base. Sepal venation three-trace, straight. Apetalous.

Holotype: S-6000, stored in the Department of Environmental Biology, University of Adelaide.

Type locality

Maslin Bay, 35 km south of Adelaide in the Willunga Sub-basin of the St Vincent Basin, South Australia.

Specimens examined

S-1786, S-840, S-1700, S-6001, S-6002.

Etymology

Named in recognition of the Maslin Bay locality which is currently outside the extant geographic range of the genus.

Description: The holotype is a fruit c. 11.5 mm in diameter with six enlarged sepals radiating around a central disk. Sepals are entire, c. 5-5.5 mm long, c. 1.5-2 mm wide, ovate-elliptic in shape with an acute to obtuse apex and a non-constricted base. Each sepal is vascularised by a central bundle with two equally prominent laterals from the receptacle wall. Weak marginal traces from the receptacle produce multiple parallel venation. Lateral veins loop and weakly anastomose with the central trace in the distal part of the sepal with intra-trace strands terminating blindly or with adjacent veins. Petals are absent. The ovary is semi-inferior, c. 2.1 mm in diameter. Styles are prominent and appear to be fused. A nectary surrounding the ovary is absent or very poorly preserved.

Ceratopetalum wilkinsonii (Ett.) Holmes & Holmes p. 268, fig. 3.

1888 *Getonites wilkinsonii* Ettingshausen p. 167-168, plate XV, fig. 12.

Emended diagnosis: Fruit five-partite. Sepals ovate-elliptic, vascularised by three prominent veins and two minor veins. Trifurcate petals occur between sepals.

Holotype: MMF8812, housed in the Geological and Mining Museum, Sydney.

Type locality

According to Holmes and Holmes (1992) and Ettingshausen (1888) the type locality is between Hill and Watson's shafts, Old Rose Valley Lead, near Emmaville in northern New South Wales.

Description: The fruit is well preserved with five enlarged, prominently vascularised sepals radiating around a central disk. Sepals are entire, c. 8-10 mm long, c.4-5.5 mm wide, ovate-elliptic in shape and constricted at the base with an obtuse apex. Calyces are vascularised by a prominent central bundle with two equally prominent laterals arising from the receptacle. Weak marginal traces also arise from the receptacle to produce multiple parallel venation (c. five veins). Laterals loop and anastomose with the central trace in the upper sepal with multiple intra-trace strands terminating blindly, with adjacent veins or at the sepal margin. The only petal present is trifurcate and intra-sepalar. The ovary is semi-inferior. The nectary is raised, probably annular and appears to have collapsed onto the sepals during preservation.

3.5 Discussion

3.5.1 Extant *Ceratopetalum* Leaf and Fruit Morphology

Leaves of *Ceratopetalum* lack any morphological features that can be used to convincingly distinguish them from those leaves of some other Cunoniaceae genera (e.g. *Schizomeria*), or even from those of other families (e.g. *Elaeocarpus*, Elaeocarpaceae). Despite this, there are some general features, such as the presence of a brachyparacytic subsidiary cell arrangement (see Table 3.2), that if they are absent can be used to reject fossil specimens as representing *Ceratopetalum.* Of particular interest, and unrelated to the fossil record, is the cuticular variability within the genus.

Table 3.2. Leaf and fruit morphological features of *Ceratopetalum* species that may be useful in identifying macrofossils

Note that satisfying the vegetative criteria does not immediately imply that the fossil specimen represents *Ceratopetalum* (see text for explanation).

Feature/structure	Description
Vegetative	
Leaves and venation	Trifoliolate or unifoliolate; semicraspedodromous secondary venation pattern; random reticulate tertiary veins. Composite intersecondary vein present, often well developed. Domatia absent.
Leaf margin	Serrations present the length of the leaf, occasionally small or reduced (e.g. *C. corymbosum*). Fimbrial vein present, well developed.
Sinus	Present, glandular and frequently prominent. Formed by the termination of a vein that originates from the secondary vein arch.
Tooth apices	Vascularised by a tertiary vein from the sinus. Spinose extension present, often prominent (*C. apetalum*) or occasionally reduced (*C. corymbosum*).
Adaxial surface	Epidermal cells isodiametric to round, non-sinuous walls.
Abaxial surface	Unornamented stomata arranged in areoles with a brachyparacytic subsidiary cell arrangement. Hydathodes present on veins. Epidermal cells isodiametric to round, non-sinuous.
Hair bases	Simple, of the 'peg' type, 5-7 radially modified epidermal cells, no or only minor basal thickening.
Reproductive	
Fruits	Enlarged sepals stellately arranged around a central disk, vascularised by 3 traces that originate from the receptacle and are not associated with the ovary. Intra-sepal marginal vein is formed by the fusion of laterals from adjacent sepals prior to entering the receptacle wall. Trifurcate petals present or absent. Ovary bicarpellate, semi-inferior and indehiscent. Diplostemonous, base of filaments present at fruit maturity.

Any phylogenetic analysis at the species level for this genus should include cuticular characters as they may prove to be informative.

In contrast to the leaves, *Ceratopetalum* fruits are highly distinctive. Diagnostic features include the presence of four to six enlarged woody sepals radiating from a central disk, a semi-inferior bi-(tri-) carpellate ovary and anthers both between and above each sepal (see Table 3.2). Sepal venation is prominently three-traced at the base where veins arise from the receptacle wall, independent of the ovary. Three-trace calyces are common to all genera of Cunoniaceae with the exception of *Pancheria* where only a single trace is present (Dickison 1975*a*). However, multiple (> 3) basal veins do occur in some *Ceratopetalum* species (e.g. *C. succirubrum* and *C. virchowii*). Dickison (1975*a*) notes the fusion of lateral traces in all Cunoniaceae calyces, but the character is extremely prominent in *Ceratopetalum* due to sepal enlargement.

3.5.2 Fossil *Ceratopetalum* Leaves

The placement of leaf macrofossils into *Ceratopetalum* has historically been based on leaf shape, secondary and tertiary venation patterns and the presence of glandular teeth apices (e.g. Ettingshausen 1888, 1890, 1894). While some of these fossils may be consistent with *Ceratopetalum*, they may be equally consistent with other genera of Cunoniaceae (e.g. *Schizomeria, Pseudoweinmannia*) or even other families. Therefore, all the previously described fossil leaf species of *Ceratopetalum* are considered here to be invalid or unverified as the original specimens could not be located for a more detailed examination of venation and cuticular morphology. Those that were directly examined for this study (*C. gilesii* and *C. macdonaldi*) are certainly invalid as the original descriptions and illustrations, upon which the identification was based, were shown to be incorrect or contained data that was misinterpreted from the original specimen. Any fossil records of *Ceratopetalum* from the Northern Hemisphere are probably misidentifications based on the extant distribution of the genus alone.

As extant *Ceratopetalum* species have relatively robust leaves it is likely that they may have been preserved as fossils. The possibility of locating fossil *Ceratopetalum* leaves is supported by the fact that several deposits have yielded fruits of the genus, which imply that the source plant must have been within a relatively short distance of the site of deposition. However, the dispersal of fruits from further afield cannot be

discounted as they possess enlarged woody sepals that make the fruit easily dispersed by wind or water (see Dickison 1984).

A major problem with studying the leaf macrofossil record of *Ceratopetalum* is the paucity of research on whole leaf architecture and cuticle morphology of other families with a similar leaf morphology, such as Elaeocarpaceae. However, even with this research it is extremely unlikely that any fossil leaf could ever be assigned to *Ceratopetalum* with confidence as there are no diagnostic morphological features available for comparison between extant and fossil specimens. At best, fossils may be excluded from the genus if they do not conform to the general features listed in Table 3.2, however if the fossil does meet all the criteria then it does not, by default, make the specimen *Ceratopetalum.* Indeed, this genus shares many leaf morphological features with other closely related genera (Table 3.3) and several that occur within the Elaeocarpaceae, and in particular, *Elaeocarpus* (see Turnbull 1986). These include semicraspedodromous secondary venation and a brachyparacytic subsidiary cell arrangement (some *Elaeocarpus*). A single distinguishing feature between some genera of Cunoniaceae and *Elaeocarpus* is in the hair bases. These are relatively unthickened in *Schizomeria, Ceratopetalum, Anodopetalum* and *Platylophus* but are extremely thickened and exserted from the leaf surface in *Elaeocarpus* (see Turnbull 1986 for illustrations). Additional research on the cuticle morphology of Elaeocarpaceae, complementing the data of Turnbull (1986), is required to satisfactorily exclude some of the existing fossil specimens previously assigned to that family as being Cunoniaceae.

3.5.3 Fossil *Ceratopetalum* Fruits

The accepted fossil *Ceratopetalum* fruit species described and reviewed in this study (Table 3.4) possess all the features considered typical of *Ceratopetalum* fruits and most notably include the presence of enlarged sepals radiating outwards from the central disk and a semi-inferior ovary which is indehiscent. Two species are petalous, *C. wilkinsonii* and *C. priscum*, while another two are apetalous, *C. maslinensis* and *C. westermannii* (Fig. 3.11). The occurrence of only one petal in the fossil of *C. wilkinsonii* (Fig. 3.10.b) is probably due to poor preservation rather than asymmetrical floral development because Cunoniaceae flowers are actinomorphic (e.g. Harden 1990*a*).

Table 3.3. Vegetative characters of *Ceratopetalum* and the closely related genera *Anodopetalum, Schizomeria* and *Platylophus*
This data is the work of the author of this thesis and is presented in Barnes and Rozefelds (2000, Appendix 1).

	Ceratopetalum	*Anodopetalum*	*Schizomeria*	*Platylophus*
Adult leaves	unifoliolate or trifoliolate	unifoliolate	simple	trifoliolate or unifoliolate
Adult leaflet form	entire	entire or lobed	entire	entire or lobed
Adult leaflet margin	serrate	serrate	serrate	serrate
Adaxial stipule colleters	present	present	present	present
Areolation	imperfect	incomplete	well developed	imperfect
Fimbrial vein	well developed	incomplete	well developed	well developed
Veinlet sheathing	sclerenchymatous	sclerenchymatous	sclerenchymatous	parenchymatous
Terminal idioblasts	present, rare	present, rare	absent	present, rare
Hydathodes	present	present	present	present
Subsidiary cell arrangement	brachyparacytic	brachyparacytic	weakly brachyparacytic	brachyparacytic

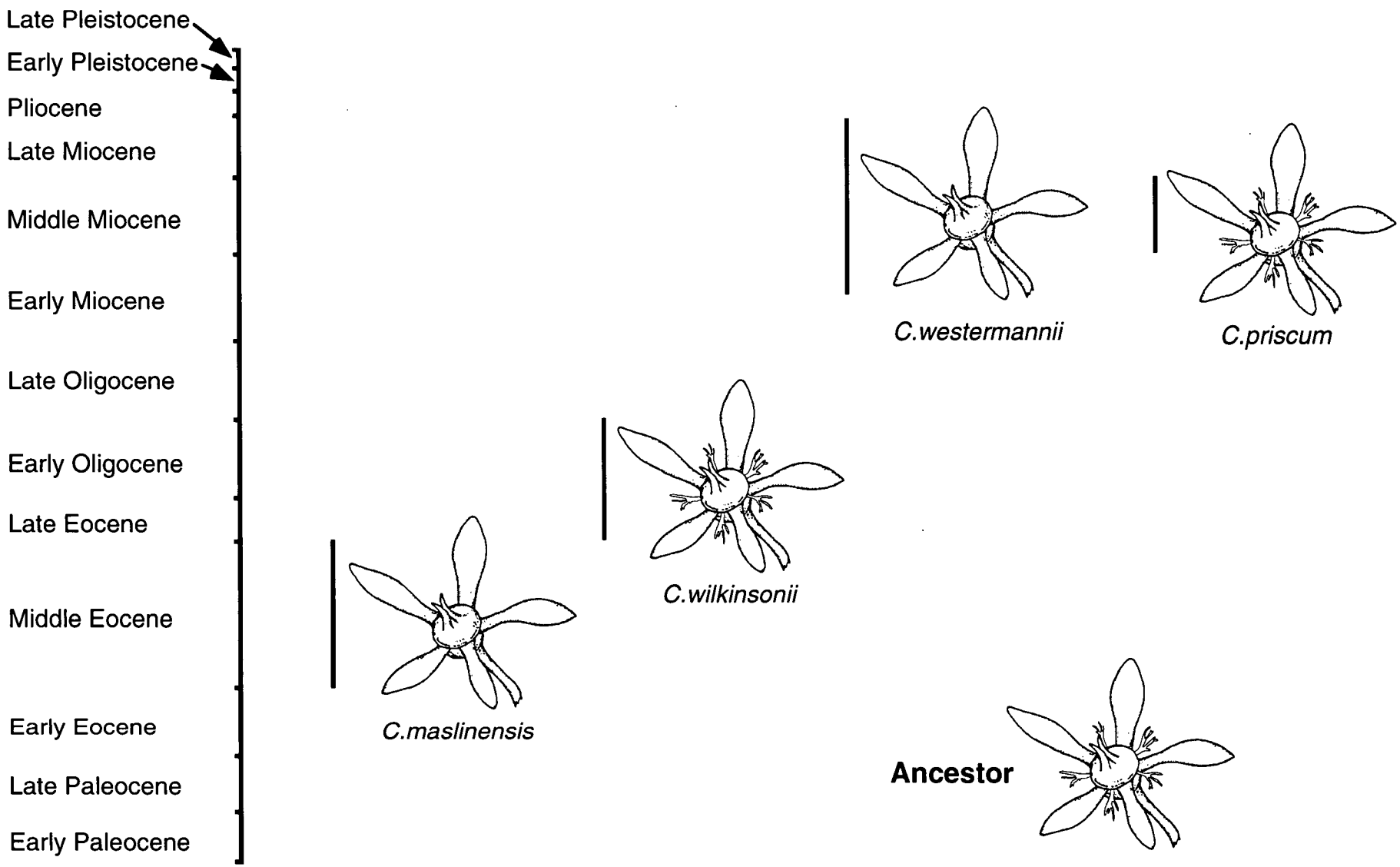
Table 3.4. Accepted macrofossil records of *Ceratopetalum*

Source: [A] this study; [B] Holmes and Holmes 1992; [C] White 1990.

Taxon	Fossil type	Geological age	Fossil locality
Ceratopetalum maslinensis [A]	Fruit compressions	Middle Eocene	Maslin Bay, South Australia
C. wilkinsonii [B]	Fruit compression	Late Eocene-Early Oligocene	Vegetable Creek, New South Wales
C. priscum [BC]	Fruit compressions	Middle Miocene	Warrumbungle Mts, New South Wales
C. westermannii [A]	Fruit compressions	late Early-Late Miocene	Elands, New South Wales

Fig. 3.11. Stratigraphic distribution and petal form of fossil *Ceratopetalum* fruits in south-eastern Australia. The line to the left of each species represents the stratigraphic age range of the deposit in which it occurs. The fruits are not drawn to scale or shape. Most species are distinguished on the presence or absence of petals, sepal shape and venation patterns.

The oldest fossil species, *C. maslinensis*, is apetalous while younger fossil species such as *C. wilkinsonii* and *C. priscum* possess tri-furcate petals. Although the oldest fossil species is apetalous the ancestral form was petalous as illustrated (see Fig. 3.12), with the secondary loss of petals occurring in at least one species by the Middle Eocene (see text for explanation).


Late Pleistocene
Early Pleistocene
Pliocene
Late Miocene
Middle Miocene
Early Miocene
Late Oligocene
Early Oligocene
Late Eocene
Middle Eocene
Early Eocene
Late Paleocene
Early Paleocene
C.westermannii
C.priscum
C.wilkinsonii
C.maslinensis
Ancestor

The presence of *Ceratopetalum* in the Middle Eocene Maslin Bay flora indicates a more widespread or different distribution of the genus during the Cainozoic (see Fig. 3.1). Its current restriction in Australia to east of the Dividing Range is probably a direct result of a changing climate because it occurs in each deposit with taxa that have their nearest relatives in the rainforests of northern or eastern Australia, or more commonly Malesia and the Pacific Islands (e.g. *Gymnostoma*, Scriven and Christophel 1990). However, due to the lack of any associations between fruit structure and the prevailing climate or vegetation type occupied by the extant species, no inferences can be made from the *Ceratopetalum* fossils as to the exact environment in which the fossil species inhabited. Based on macroflora assemblages, all fossil species probably occurred in rainforest or wet sclerophyll vegetation (e.g. Holmes *et al.* 1983; Hill and Whang 2000).

3.5.4 Petal Evolution in *Ceratopetalum*

The origin of petals in the Cunoniaceae has received some attention by various authors (e.g. Ehrendorfer *et al.* 1984; Dickison 1989) but has not been adequately resolved. Ehrendorfer *et al.* (1984) suggest a secondarily derived staminal origin of petals in Cunoniaceae based on petal position and the fact that both stamens and petals are vascularised by a single trace (see also Dickison 1975*a*), which is a hypothesis that is also supported by the presence of one trace petaloid stamens in *Bauera* (Prakash and McAlister 1977).

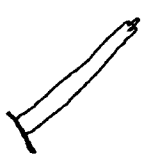
Hufford and Dickison (1992) suggest tri-furcate petals are independently derived in *Platylophus* and an *Anodopetalum-Ceratopetalum-Schizomeria* clade. However, a revised family phylogeny (Bradford and Barnes manuscript submitted, Appendix 1) and a comparative morphological study of *Anodopetalum* (Table 3.3; Barnes and Rozefelds 2000, Appendix 1) suggest all four genera represent a monophyletic clade, termed the Schizomerieae tribe (Fig. 3.12). *Platylophus, Schizomeria* and a single species of *Ceratopetalum* possess prominent tri-furcate petals (see Fig. 3.12) while those of *Anodopetalum* are only slightly notched at the apex (Barnes and Rozefelds 2000, Appendix 1).

The ancestor to Schizomerieae was petalous based on the cladogram of Bradford and Barnes (manuscript submitted, Appendix 1; Fig. 3.12). Therefore, the oldest *Ceratopetalum* fossil fruit (*C. maslinensis*) does not represent the oldest *Ceratopetalum* species as it is apetalous (Fig. 3.11). This implies that the *Ceratopetalum* must have

Fig. 3.12. A cladogram of the genera within the tribe Schizomerieae. This cladogram is a subsection of the strict consensus tree produced from a parsimony analysis of morphological characters at the generic level for all Cunoniaceae genera using a constraint tree based on clades supported by molecular data (see Bradford and Barnes manuscript submitted, Appendix 1).

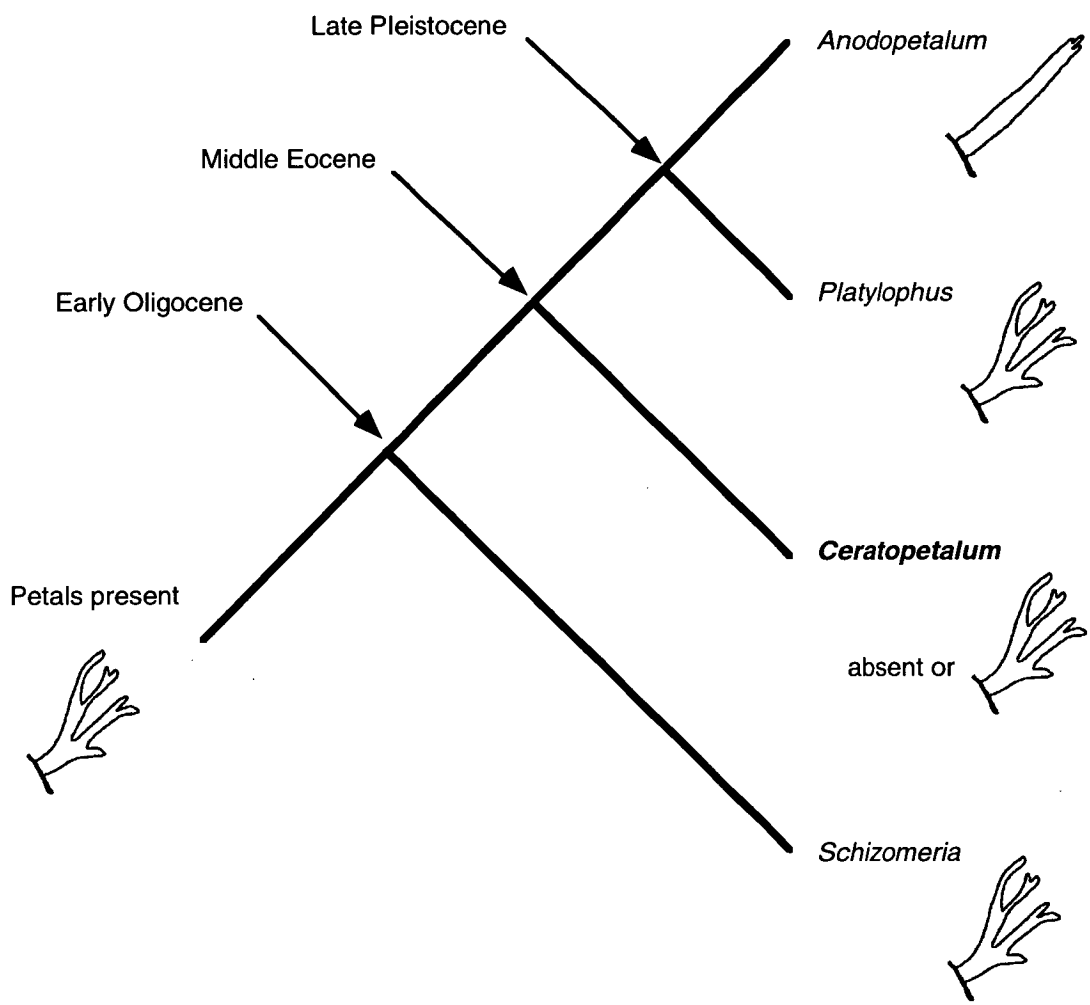
The petal form for each extant genus is shown to the right of the generic name (see below for explanation of symbols). All genera have apically incised petals. *Ceratopetalum gummiferum* is the only species in that genus to have petals as all other species are apetalous. Based on parsimony the ancestor to the clade had deeply incised petals.

The minimum ages for each node are based on the macrofossil record of each genus (*Schizomeria*, Carpenter and Buchanan 1993; *Ceratopetalum*, this study; *Anodopetalum*, Jordan *et al.* 1991). The oldest *Ceratopetalum* fossil fruit shows that the secondary loss of petals had occurred by the Middle Eocene at the latest. The age of the *Ceratopetalum* lineage implies that the *Schizomeria* clade is at least Middle Eocene in age despite the Early Oligocene age of the oldest known fossil (*Schizomeria tasmaniensis*, Cethana).



Petals present with shallow incisions towards the apex.

Petals present with deep and irregular incisions towards the apex.


Late Pleistocene
Middle Eocene
Early Oligocene
Petals present
Anodopetalum
Platylophus
Ceratopetalum
absent or
Schizomeria

radiated prior to or during the Middle Eocene, with the potential for petalous fruits at least to be present in deposits older than or the same age as Maslin Bay. The only slightly younger *C. wilkinsonii* has a single tri-furcate petal preserved, and more recent fossils being both petalous (*C. priscum*) and apetalous (*C. westermannii*). Clearly, the presence of tri-furcate petals in two fossil species indicates petally was once more widespread in the genus (Fig. 3.11), but the loss of petals had occurred in at least one species by the Middle Eocene (*C. maslinensis*).

The secondary loss of petals in different lineages of the family has been suggested by Dickison (1989), and particularly in *Ceratopetalum*, to have occurred by the specialisation of the fruit or a change in pollination vector (entomophily to anemophily). Numerous Cunoniaceae are insect pollinated and have flowers with large petals and well developed nectaries that secrete a sweet smelling exudate (e.g. *Eucryphia*) while others are wind pollinated (Dickison 1989). The development of apetally in *Ceratopetalum* may indicate a change from a winged to a terrestrial insect pollinator or a complete shift back to anemophily, in which case the petals have then become more or less redundant in attracting insects, if they served this function at all given their small size. The strong development of basally constricted lobed sepals in all extant and some fossil species suggests an evolutionary advancement to improve seed aerodynamics as they are wind dispersed (Dickison 1984, 1989). The description of more fossil fruits of *Ceratopetalum* may enable a more detailed evaluation of floral evolution to be made.

Chapter 4. Macrofossils of *Callicoma* and *Codia*

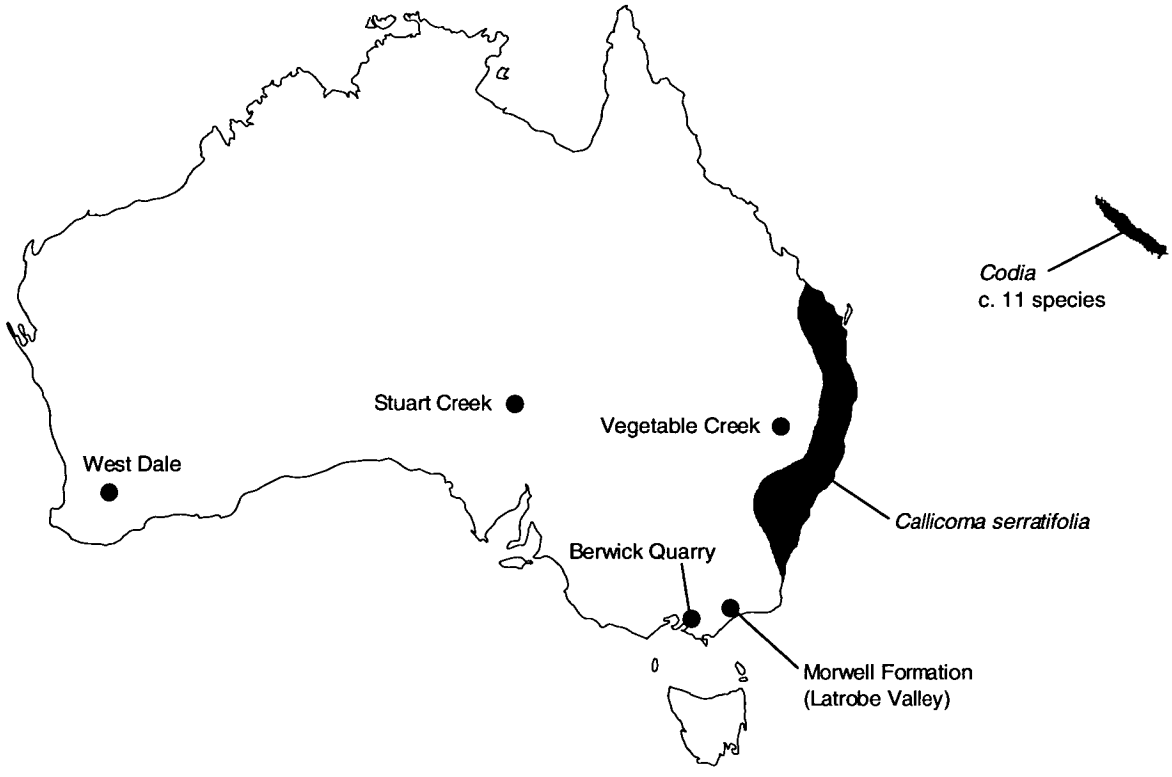
4.1 Introduction

Callicoma is one of seven genera endemic to Australia and is represented by a single extant species, *C. serratifolia* Andrews (Harden 1990*a*). *Callicoma serratifolia* is a large canopy to sub-canopy tree of disturbed forest habitats, creeklines and poorer soils of eastern Australia (Fig 4.1; Floyd 1989; Harden 1990*a*). The species has opposite decussately arranged leaves that are very coarsely serrate, and persistent interpetiolar stipules (Fig. 4.2.a). Flowers are clustered into axillary ball inflorescences (Fig. 4.2.b) that are most commonly single, but do occasionally occur in pairs or as small clusters on the same peduncle (Kennedy and Prakash 1981; Floyd 1989). Flowers are pentamerous, diplostemonous, apetalous and possess a hypogynous bi(tri)carpellate ovary (Kennedy and Prakash 1981; Harden 1990*a*). Carpels dehisce upon maturity to release several small, round seeds that have a papillate-tuberculate coat (Kennedy and Prakash 1981; Dickison 1984; Carpenter and Buchanan 1993).

Various aspects of the leaf and floral morphology (Dickison 1975*a*, 1975*b*, 1980*a*; Kennedy and Prakash 1981) and embryological development (Kennedy and Prakash 1981) of *C. serratifolia* have been studied extensively, with two leaf morphotypes identified but not given taxonomic status (Table 4.1; Kennedy and Prakash 1981). The morphotypes are distinguished primarily on the number of orders of leaf serrations, trichome type and distribution patterns, and stem pubescence. The number of bars per perforation plate was also shown to vary between the two morphotypes (see Kennedy and Prakash 1981), but this character is impractical to distinguish them in the field. Generally, the wood anatomy of *C. serratifolia* has been well discussed by Dadswell and Eckersley (1938), Metcalfe and Chalk (1950), Ingle and Dadswell (1956), Dickison (1980*b*) and Kennedy and Prakash (1981).

Codia is a genus of approximately 11 species (Guillaumin 1948) which grow mainly as small shrubs in the scrubby, sclerophyllous maquis vegetation of New Caledonia (Specht 1979; Rao and Dickison 1985*b*). *Codia* is poorly known in the literature with scant information on wood (Dickison 1980*b*), leaf (Dickison 1975*b*), floral and seed (Baker 1921; Guillaumin 1948; Dickison 1975*a*, 1984) morphology. Mature plants possess opposite decussate leaves with entire margins and interpetiolar stipules that are caducous and leave a prominent scar (Fig. 4.2.c). The flowers of *Codia* are arranged

Fig. 4.1. Map of Australia and New Caledonia showing the approximate extant distribution of *Callicoma serratifolia* and *Codia* species (shaded). Three fossil localities (circles) occur within Tasmania (inset) while all others occur on mainland Australia.


Codia
c. 11 species
Stuart Creek
Vegetable Creek
West Dale
Callicoma serratifolia
Berwick Quarry
Morwell Formation
(Latrobe Valley)

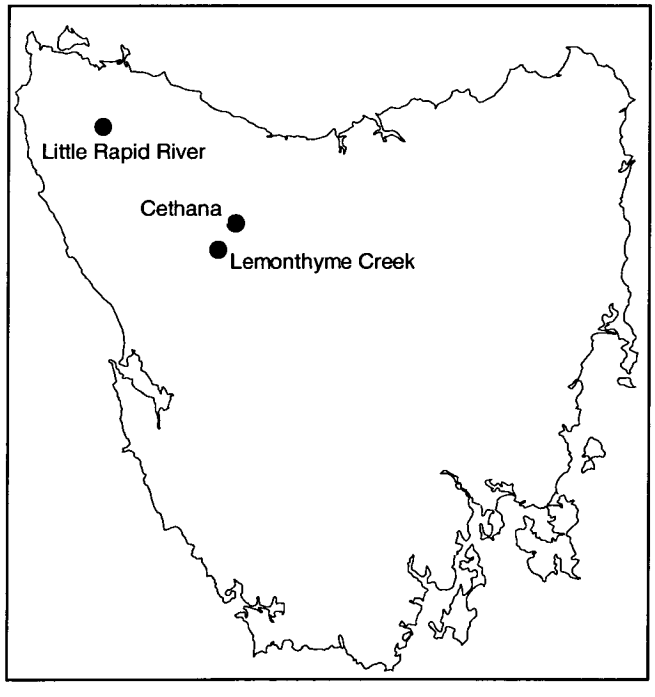

Little Rapid River
Cethana
Lemonthyme Creek

Fig. 4.2.a. Leaf form and phyllotaxy in *Callicoma serratifolia.* Leaves are opposite and decussately arranged with prominent interpetiolar stipules (arrow). New growth is densely pubescent. Scale bar = 10 mm.

Fig. 4.2.b. Ball inflorescence of *C. serratifolia.* Flowers are clustered into a dense ball with stamens well protruded (right inflorescence). Note the prominent styles (arrow) that extend well beyond the flowers whilst the anthers are still immature. Scale bar = 10 mm.

Figs 4.2.c-e. Leaf form and floral morphology of *Codia montana.* Scale bar for all = 10 mm.

Fig. 4.2.c. Shoot showing opposite decussate leaf arrangement and prominent interpetiolar scar on stem (arrow). Leaves have entire margins.

Fig. 4.2.d. Ball inflorescences in an axillary position showing long peduncle.

Fig. 4.2.e. Individual fruits are indehiscent and are shed from the spherical head upon maturity. Note the remnant peduncle almost denuded of fruits (black arrow) and a dorsal view of a fruit showing persistent sepals at the base of the fruit (white arrow).

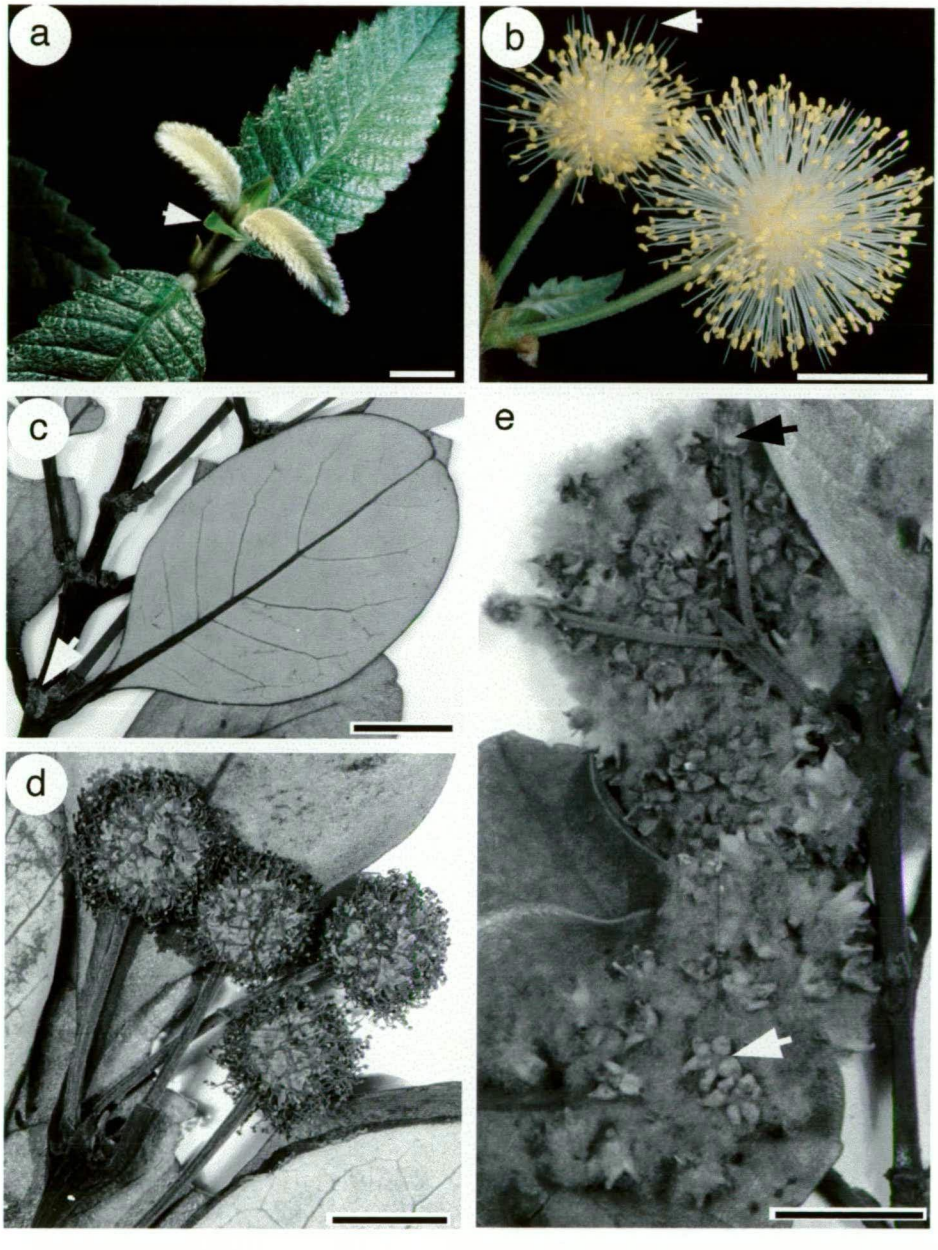

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Table 4.1. Morphological characters identified by Kennedy and Prakash (1981) to separate *Callicoma serratifolia* into Group A and B morphotypes

	Group A	Group B
Marginal teeth	Single	Double
Trichomes	Curly	Curly and straight
Venation	Craspedodromous	Cladodromous
Tertiary venation	Oblique angle	Outward oblique angle
Veinlets	Simple and linear	Once branched
Colleters	Absent	Present between stem and petiole

into dense spherical heads and occur in the leaf axils in the upper portion of the plant (Fig. 4.2.d; Engler 1928; Guillaumin 1948). Fruits at maturity are shed from the peduncle with each individual fruit being an indehiscent capsule with the sepals persisting at the base (Fig. 4.2.e; Dickison 1984). The outer surface of each fruit is densely covered with long woolly hairs (Fig. 4.2.e).

The taxonomic relationships of *Callicoma* and *Codia* have been unclear, often appearing as contradictory interpretations in the literature. For example, Engler (1928) placed *Callicoma, Codia* and *Pancheria* into the tribe Pancherieae which is characterised by flowers clustered into ball-like heads. Hufford and Dickison (1992), in a phylogenetic analysis of Cunoniaceae, indicated Pancherieae is polyphyletic which supports the initial view of Dickison (1984, 1989) that the tribe represents floral convergence as anatomical (wood) and morphological (calyx aestivation, perianth, fruit and seed type) attributes do not support tribe monophyly. However, a major problem with all phylogenetic analyses of Cunoniaceae is the difficulty in scoring homologous structures which do not represent convergence (e.g. Hufford and Dickison 1992; Rutishauser and Dickison 1990). This is especially true for the tribe Pancherieae (Engler 1928) as flowers aggregated in ball-like heads may indeed represent floral convergence as advocated by Dickison (1984, 1989). Rutishauser and Dickison (1990) have hypothesised the tribe may well be a natural one but that this is difficult to demonstrate as floral homologies among the genera are difficult to score.

In any case, the status of Pancherieae appears doubtful as *Pancheria* formed a monophyletic clade with *Weinmannia* and *Cunonia* in the analysis of Hufford and Dickison (1992) and in recent molecular studies (Bradford 1998). Although this does not necessarily imply that *Codia* and *Callicoma* are unrelated, the analysis of Hufford and Dickison (1992) produced no clear autapomorphies for *Callicoma* and indicated that it is the sister taxon to *Caldcluvia* sensu stricto, a monotypic genus restricted to South America (Zegers 1995). *Codia*, which included *Pullea* in the study of Hufford and Dickison (1992), was nested in a clade with the South Pacific genera *Anodopetalum, Schizomeria, Ceratopetalum* and South African *Platylophus*. There are several inaccuracies within the data matrix of Hufford and Dickison (1992), most noticeably the fact that *Codia* was combined with *Pullea* into a single terminal taxon with the autapomorphy of indehiscent fruits with an undifferentiated seed coat. These taxa should not be lumped as mature *Codia* leaves are entire with brochidodromous venation whilst those of *Pullea* are almost always serrate with predominantly semicraspedodromous venation, but only the latter state was recognised by Hufford and Dickison (1992). Other scoring inaccuracies of *Callicoma* and *Codia* (including *Pullea*) include, for example, leaf arrangement (character no. 3), stomata (character no.

11), inflorescence type (character no. 23), pollen aperatures (character no. 29) and the seed surface (character no. 42). A revised family phylogeny based on molecular and corrected morphological data, to which this study contributed, shows that *Codia* (excluding *Pullea*) and *Callicoma* are sister taxa (Bradford and Barnes manuscript submitted, Appendix 1).

Macrofossils from at least five Australian Cainozoic fossil localities (Ettingshausen 1888; Blackburn 1985; Carpenter and Buchanan 1993; Hill and Merrifield 1993; Pole *et al.* 1993) have either been assigned to, or considered to have affinities with, extant *Callicoma* (Table 4.2). No microfossil studies have specifically detected *Callicoma* pollen, probably due to its similarities with other dicolporate genera of the family (e.g. *Acrophyllum, Pullea* and *Pseudoweinmannia*). *Codia* has not been reported as a macro- or microfossil.

This study aims to review selected aspects of leaf and floral morphology of *Callicoma serratifolia* and some *Codia* species to identify palaeobotanically and phylogenetically informative characters. A review of six existing macrofossil records and macrofossils from two new localities, all considered to represent *Callicoma*, are presented. The first macrofossil of *Codia* is described.

4.2 Materials and Methods

4.2.1 Leaf and Cuticle Morphology of Extant Species

Mature foliage, inflorescences and infructescences of *Callicoma serratifolia* and six *Codia* species (*C. albifrons, C. discolor, C. montana, C. nitida, C. obcordata* and *C. spathulata*) were obtained from herbarium specimens from the Australian National Herbarium (CANB), Herbarium of South Australia (AD), Tasmanian Herbarium (HO), Missouri Botanical Gardens (MO) and the University of Minnesota Herbarium (MU) and the collection at the School of Plant Science, University of Tasmania. Refer to Appendix 3 for a complete list of specimens examined in this study.

Specimens covered the geographic range of both genera. Leaves from mature trees and seedlings of *C. serratifolia* were also available from specimens cultivated at the University of Tasmania. A single seedling of an indeterminate *Codia* species, collected from Rivieré Pirogues in New Caledonia by R. J. Carpenter, was also available (HO 444879).

Table 4.2. Previously described macrofossil records of *Callicoma*

Source: [A] Unger 1866; [B] Ettingshausen 1888; [C] Hill and Merrifield 1993; [D] Carpenter and Buchanan 1993; [E] Pole *et al.* 1993; [G] Greenwood *et al.* 1990; [H] Rowett 1997.

Taxon	Fossil type	Geological age	Fossil locality
Callicoma pannonica [A]	Leaf impression	Tertiary	Eperies, Austro-Hungary
C. primaeva [B]	Leaf impression	Eocene	Vegetable Creek, New South Wales
cf. *Callicoma* [C]	Mineralised, incomplete leaf	Middle Eocene-Oligocene	West Dale, Western Australia
C. serratifolia [D]	Leaf compression	Early Oligocene	Cethana, north-central Tasmania
C. serratifolia [D]	Infructescence compression	Early Oligocene	Cethana, north-central Tasmania
sp. '*Callicoma*' [E]	Leaf compressions	Late Oligocene	Berwick Quarry, Victoria
aff. *Callicoma* [F]	Dispersed cuticle	Oligocene-Early Miocene	Morwell Formation, Victoria
'Serrate-coarse' (*Callicoma*?) [GH]	Leaf impression in silcrete	Miocene to Pliocene	Stuart Creek, South Australia

4.2.2 Fossil Localities and Specimens

Detailed fossil site descriptions are provided in '2.5 Fossil Localities, Geological Ages and Specimens'. Macrofossils examined in this study were compared to the extant specimens used in the morphological study. Fossil localities are shown in figure 4.1.

4.2.2.1 Little Rapid River, north-western Tasmania

Several mummified leaves, leaf fragments and two complete infructescences composed of >20 individual fruits that are assignable to *Callicoma* were extracted from the Early Oligocene sediments and examined during this study.

4.2.2.2 Berwick Quarry, Victoria

The Oligocene to possibly earliest Early Miocene Berwick Quarry macroflora has been studied by Deane (1902*a*) and Pole *et al.* (1993). The *Lomatia* species of Deane (1902*a*) were described as 'probably Cunoniaceae' by Pole *et al.* (1993). The three leaf macrofossils described as ?Cunoniaceae sp. '*Callicoma*' by Pole *et al.* (1993) were available for this study.

4.2.2.3 Stuart Creek (Eyre Formation), South Australia

The age of the leaf-bearing silcrete overlaying the Willalinchina sandstone is uncertain with a probable Miocene to Pliocene age (Rowett 1997). A single rock preserving a silcrete leaf impression (R364695) and a latex mould of an *in situ* leaf impression (Fossil Leaf Type No. 3) were examined in the laboratory as all other field examined specimens were uncollectable and remain *in situ.*

4.2.2.4 Lemonthyme Creek core, north-western Tasmania

Three incomplete, coalified leaf compressions of *Callicoma* were extracted from the Early Oligocene Lemonthyme Creek core (see Macphail *et al.* 1993).

4.2.2.5 Cethana, north-central Tasmania

A single specimen each of a leaf and infructescence of the extant *Callicoma serratifolia*

have been described by Carpenter and Buchanan (1993) from this Early Oligocene deposit (Carpenter and Hill 1988). The specimens examined by Carpenter and Buchanan (1993) were available for this study and were supplemented with additional specimens located in the Cethana sediment housed at the School of Plant Science, University of Tasmania.

4.2.2.6 Vegetable Creek, New South Wales

Ettingshausen (1888) described a single leaf impression as *Callicoma primaeva* from Vegetable Creek (now Emmaville), New South Wales. The illustration and description by Ettingshausen (1888) were available for this study but the original specimen could not be located.

4.2.2.7 Eperies, Austro-Hungary, Europe

The illustration and description by Unger (1866) of *Callicoma pannonica* were available for this study but the original specimen could not be located.

4.2.2.8 West Dale, south-western Western Australia

A single mineralised leaf from this Middle Eocene-Oligocene deposit was assigned to cf. *Callicoma* by Hill and Merrifield (1993). This was based on leaf shape and the presence of a ridge of cutin around the stomatal pore but the paired hair bases characteristic of extant *Callicoma* were not located. The prepared sample and photographs examined (WAM P.88.84A) by Hill and Merrifield (1993) were available for this study.

4.2.2.9 Morwell Formation, Latrobe Valley, Victoria

Blackburn (1985) described dispersed cuticle as Cunoniaceae aff. *Callicoma* from a single sample of medium light lithotype in the Oligocene-Early Miocene Morwell Formation. The description and illustrations by Blackburn (1985) were available for this study.

4.3 Results

4.3.1 Extant Morphology of *Callicoma serratifolia*

Diagnostic morphological features of *Callicoma serratifolia* are listed in Table 4.3. Leaves from mature and immature plants are simple, elliptic to ovate, with an acute to cuneate base and an acute to acuminate apex (Fig. 4.3.a-b). Secondary venation is strongly craspedodromous (Fig. 4.3.a-b) with veins terminating at a glandular-mucronate apex or occasionally bifurcating and terminating at different teeth (e.g. Fig. 4.3.a). Secondary veins are straight, numerous, 12-35 per leaf, and are not curved apically in the lower part of the leaf or basally deflected near the sinus (e.g. Fig. 4.3.a-b). The margin is regularly serrate, commonly with single teeth (Fig. 4.3.b-c) but sometimes with double and triple teeth which are formed by the termination of a tertiary vein at the leaf margin between the tooth apices vascularised by secondary veins (Fig. 4.3.d-e). In all leaves, there is a glandular pubescent sinus that is formed by the convergence of tertiary veins (e.g. Fig. 4.3.c-e). The cladodromous venation reported by Kennedy and Prakash (1981) is absent. Tertiary veins are strongly to weakly percurrent (Fig. 4.3.a-e) with random reticulate higher order venation.

Areolation is imperfect with pentagonal to quadrangular areoles 300-800 μm in diameter (Fig. 4.3.f). Veinlet endings are variable in length, 100-250 μm long, once or twice branched with occasional terminal idioblasts (Fig. 4.3.f-g). Leaves are pubescent, often appearing white on the abaxial surface due to small curly hairs on the lamina while large unicellular hairs occur on the midrib, secondary veins and, occasionally, on higher veins and areoles of some leaves (Fig. 4.3.h). The distribution of these hairs varies within the species but exhibits no correlation to any other morphological character, habitat or geographic origin.

Abaxial epidermal cells are isodiametric to round with non-sinuous, smooth walls (Fig. 4.4.a-b). Stomata are present and variable in size, ranging from 20-28 μm in length, and have a prominent wavy frill of cutin around the stomatal apparatus (Fig. 4.4.b-c) and are randomly arranged in areoles (Fig. 4.4.b). Subsidiary cell arrangement is more or less anomocytic (Fig. 4.4.b). Two hair types are present. Small paired, curly and thinly cutinised hairs are associated with the stomata (Fig. 4.4.c) and have a simple, thinly cutinised rim. The second type are long, thick unicellular hairs present mainly on major and minor veins (Fig. 4.4.a) and the midrib (Figs 4.3.h and 4.4.d). Hair bases are simple, surrounded by 5-7 radially modified

Figs 4.3.a-b. Extant leaves of *Callicoma serratifolia.* Scale bar for both = 10 mm.

Fig. 4.3.a. Leaf from immature plant. Secondary veins occasionally bifurcate and terminate at different teeth (arrow).

Fig. 4.3.b. Leaf from mature plant.

Figs 4.3.c-e. Serrations in mature leaves of *C. serratifolia.* Note glandular sinus formed by the convergence of tertiary veins (arrows). Scale bar for all = 10 mm.

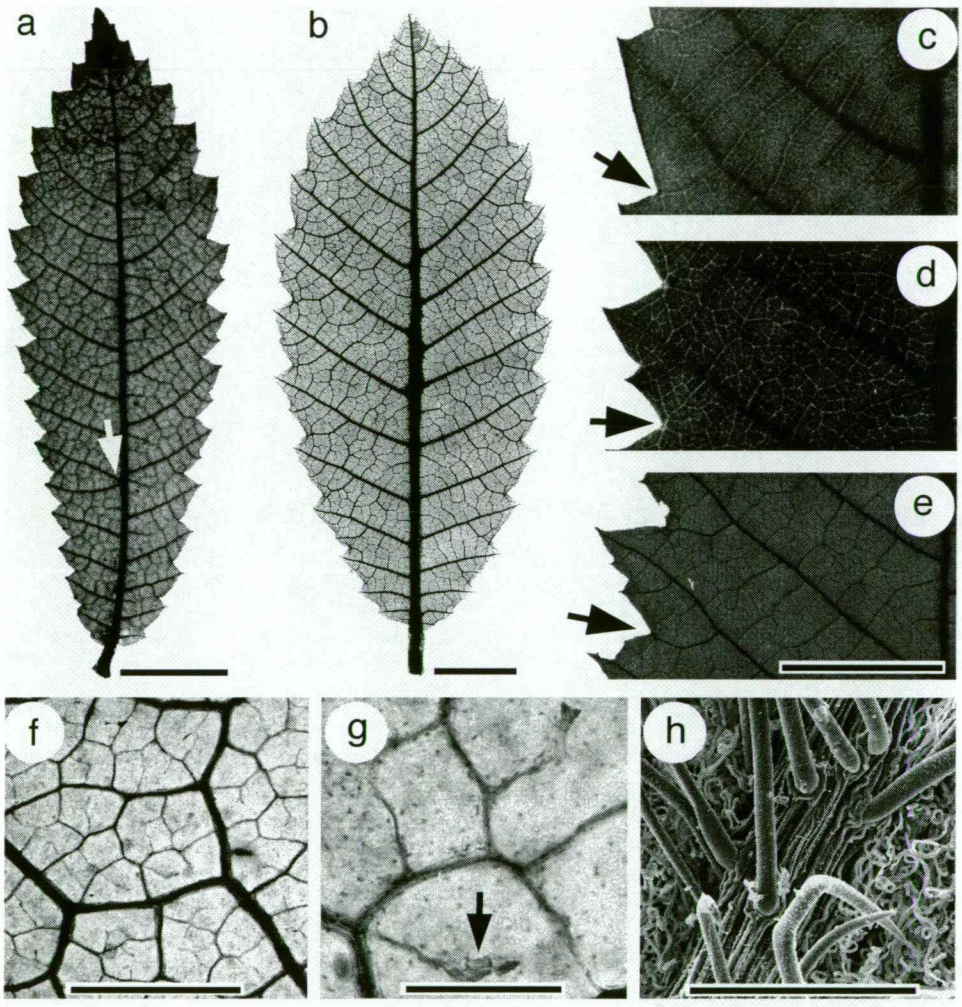
Fig. 4.3.c. Single. **Fig. 4.3.d.** Double. **Fig. 4.3.e.** Triple.

Figs 4.3.f-g. Light micrographs of cleared *C. serratifolia* leaves.

Fig. 4.3.f. Imperfect areolation with once or twice branching veinlets. Scale bar = 1 mm.

Fig. 4.3.g. Veinlets showing uncommon square terminal idioblasts (arrow). Scale bar = 100 μm.

Fig. 4.3.h. Scanning electron micrograph of the outer abaxial midrib showing unicellular hairs and ribbed epidermal cells. Paired thinly cutinised curly hairs occur in areoles. Scale bar = 300 μm.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Figs 4.4.a-f. Cuticular features of *Callicoma serratifolia.*

Figs 4.4.a-b. Light micrographs of the abaxial surface. Scale bar for both = 50 μm.

Fig. 4.4.a. Areole showing stomata and large unicellular hair bases with no basal cell (arrow).

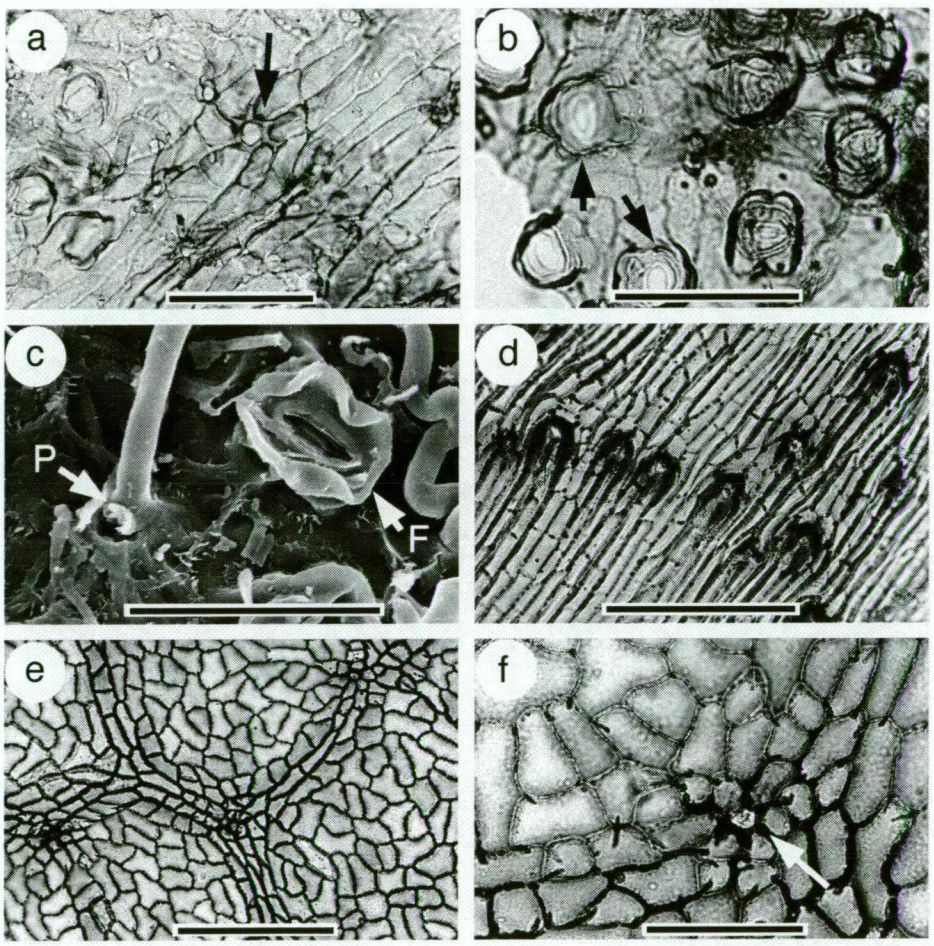
Fig. 4.4.b. Stomata with a cutin frill (arrows) and anomocytic subsidiary cells.

Fig. 4.4.c. Scanning electron micrograph of a stoma showing cutin frill (F) and small paired hair bases (P) with a single hair still attached. Scale bar = 30 μm.

Fig. 4.4.d. Light micrograph of the abaxial midrib showing elongated venal cells with slightly exserted unicellular hair bases. Scale bar = 200 μm.

Fig. 4.4.e. Light micrograph of the adaxial surface. Scale bar = 200 μm.

Fig. 4.4.f. Light micrograph of an adaxial unicellular hair base (arrow) with radial epidermal cells and no foot cell. Scale bar = 50 μm.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and slightly thickened epidermal cells but with no basal cell (Fig. 4.4.a). The abaxial midrib cells are elongated and raised giving a ribbed appearance with unicellular hair bases slightly exserted (Fig. 4.4.d).

On the adaxial surface epidermal cells are isodiametric to quadrangular with non-sinuous, smooth or slightly pitted walls (Fig. 4.4.e). Epidermal cells are randomly arranged in the areoles and occur between elongated, rectangular venal cells which are narrow and have non-sinuous walls (Fig. 4.4.e). The surface is non-ornamented but the venal cells are slightly ribbed and raised in outline. Large unicellular hairs are present and are most common on the midrib and major veins with hair bases as above (Fig. 4.4.f).

Bisexual flowers are arranged in a ball inflorescence (Fig. 4.2.b), 15-25 mm in diameter. Flowers have 4-6 triangular sepals, an ovary of 2(-3) fused superior carpels, no petals and no nectary disk. Fruits remain in the clustered head at maturity (Fig. 4.5.a). The sepals and ovary are pubescent, with both large unicellular and small paired, thinly cutinised hairs present (Fig. 4.5.b) with bases identical to those on the abaxial leaf surface (see Figs 4.3.h and 4.4.c). The glandular trichomes reported to be on the sepals and ovary wall by Kennedy and Prakash (1981) are absent. Stomata are rare on the sepal surface and are surrounded by a cutin frill (Fig. 4.5.c), similar to the stomata on the abaxial leaf surface (cf. Fig. 4.4.c). The mature fruit is a capsule that dehisces ventrally along the inner ledge (see also Bentham and Mueller 1864; Harden 1990*a*) without a vascular connective persisting between the dehisced carpels (see Fig. 4.5.a), as present in some Cunoniaceae genera (e.g. *Caldcluvia*; see Godley 1983). Seeds are round with a tuberculate-papillate seed surface (Bentham and Mueller 1864; Kennedy and Prakash 1981; Dickison 1984; Carpenter and Buchanan 1993).

4.3.2 Extant Morphology of Juvenile *Codia* Leaves

The leaf morphology of *Codia* is highly variable with a juvenile leaf phase occurring in some species (see Guillaumin 1948). Some vegetative structures present in the juvenile foliage are also present in the adult foliage of some species. The node of phase change could not be determined from the single seedling as the adult foliage was absent.

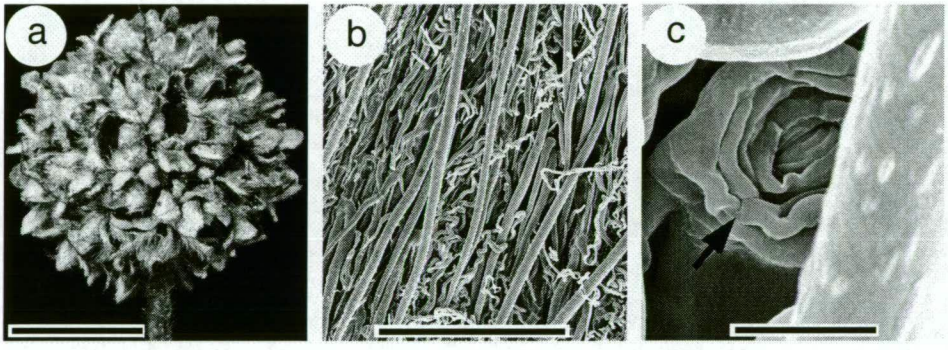
The juvenile leaves of the single specimen examined have single and regular serrations in the upper leaf associated with craspedodromous secondary venation while brochidodromous venation occurs where serrations are absent (Fig. 4.6.a). Tertiary

Fig. 4.5.a. Infructescence of *Callicoma serratifolia*. Scale bar = 10 mm.

Figs 4.5.b-c. Scanning electron micrographs of the sepal surface of *C. serratifolia.*

Fig. 4.5.b. Abaxial surface showing two hair types; thick, straight hairs and thinly cutinised curly hairs, similar to those that occur on the abaxial leaf surface. Scale bar = 200 μm.

Fig. 4.5.c. Stoma on the sepal showing multiple cutin frill (arrow). Scale bar = 20 μm.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Figs 4.6.a-g. *Codia* juvenile leaf characters.

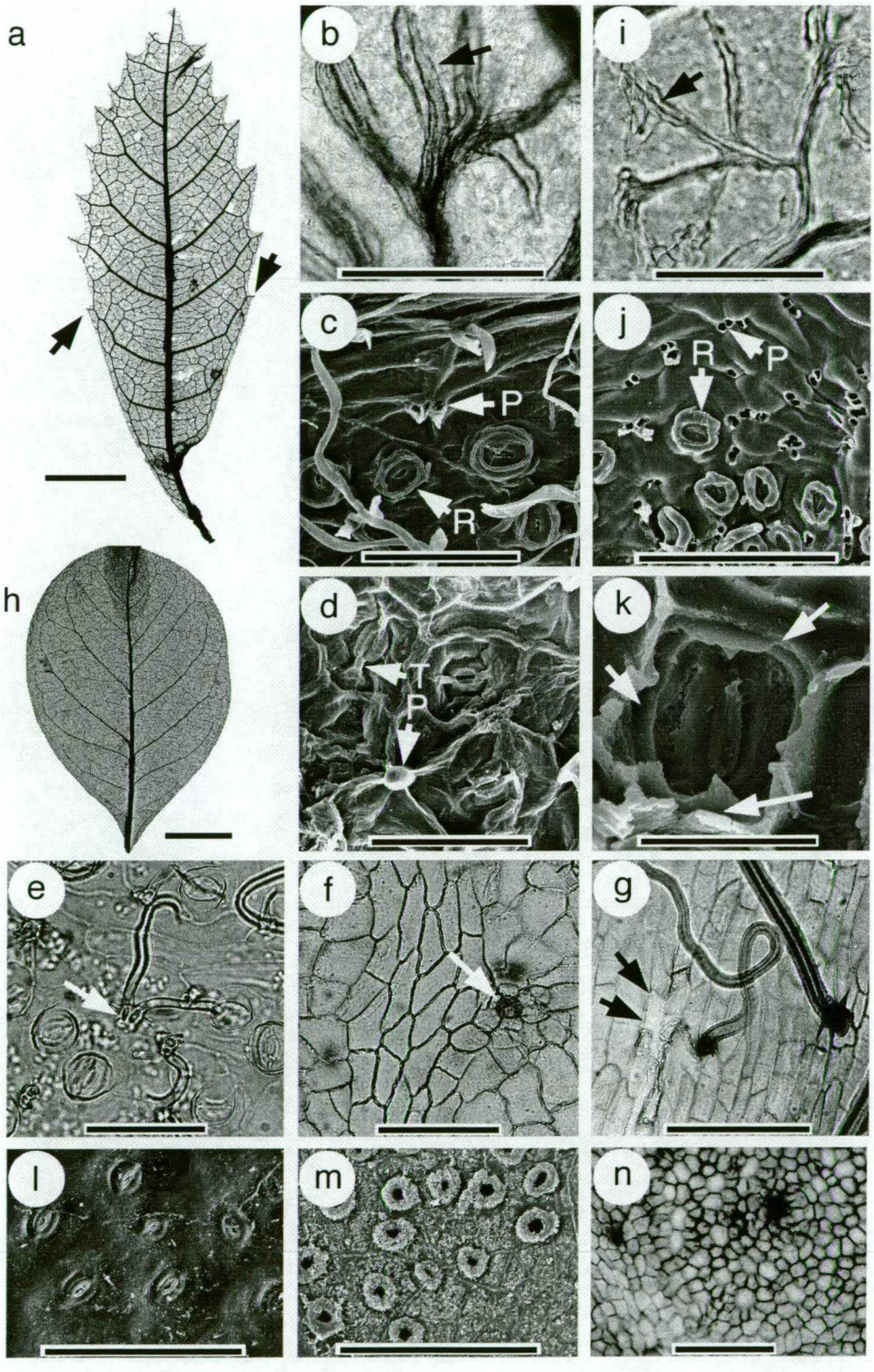
Fig. 4.6.a. Cleared leaf showing venation and basal serrations vascularised by a basally deflected vein (arrows). Scale bar = 10 mm.
Fig. 4.6.b. Light micrograph of tubular terminal idioblasts on veinlets (arrow). Scale bar = 300 µm.
Fig. 4.6.c. Scanning electron micrograph of the outer abaxial cuticle showing stomatal cutin ring (R) and small paired hair bases (P). Scale bar = 50 µm.
Fig. 4.6.d. Scanning electron micrograph of the inner abaxial cuticle showing weakly anisocytic stomata with t-pieces (T) at each pole and paired hair bases (P). Scale bar = 40 µm.
Fig. 4.6.e. Light micrograph of the abaxial cuticle showing paired hair bases (arrow). Scale bar = 50 µm.
Fig. 4.6.f. Adaxial cuticle showing non-ribbed venal cells. Unicellular hair bases are uncommon and have a foot cell (arrow). Scale bar = 50 µm.
Fig. 4.6.g. Abaxial midrib. Unicellular hairs with a foot cell (right) and unpaired (centre) thinly cutinised curly hairs are present. Paired hairs are uncommon and have non-thickened bases (arrows indicate hair bases). Scale bar = 150 µm.

Figs 4.6.h-k. *Codia discolor* adult leaf characters.
Fig. 4.6.h. Cleared leaf. Scale bar = 10 mm.
Fig. 4.6.i. Light micrograph of tubular terminal idioblasts on veinlets (arrow). Scale bar = 300 µm.
Fig. 4.6.j. Scanning electron micrograph of the outer abaxial cuticle showing stomatal cutin ring (R) with paired hair bases (P). Scale bar = 50 µm.
Fig. 4.6.k. Inner cuticular surface of a stoma showing narrow band of subsidiary cells of the anisocytic type (arrows). Scale bar = 20 µm.

Fig. 4.6.l. Scanning electron micrograph of the outer abaxial cuticle of adult *C. nitida*. Scale bar = 100 µm.

Fig. 4.6.m. Scanning electron micrograph of the outer abaxial cuticle of adult *C. montana*. Scale bar = 100 µm.

Fig. 4.6.n. Light micrograph of the adaxial cuticle of adult *C. montana* showing star configuration of epidermal cells over areoles. Scale bar = 200 µm.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veins are weakly percurrent with a sinus absent or, when present, it is in the upper portion of the leaf and weakly formed by branches of the secondary laterals. However, these often fuse within the leaf margin to form a semicraspedodromous pattern (Fig. 4.6.a). Basal secondary veins are curved apically and terminate at small teeth with the vein near the sinus basally deflected (see arrows in Fig. 4.6.a). Areolation is incomplete with veinlets 1-3 branched and terminating with tubular idioblasts (Fig. 4.6.b).

Stomata are surrounded by a cutin ring rather than a ledge or frill of cutin, which is present in the adult leaves of some species, and are randomly arranged in areoles with small, paired hairs (Fig. 4.6.c-e). Subsidiary cell arrangement is weakly anisocytic, with a prominent t-piece at each stomatal pole (Fig. 4.6.d). Adaxial epidermal cells are isodiametric with non-sinuous, non-pitted walls which are arranged between scarcely pubescent veins (Fig. 4.6.f). Hair bases are surrounded by 5-7 radially modified epidermal cells with a basal cell present (Fig. 4.6.f). Abaxial midrib cells are elongated but relatively short and not ribbed (Fig. 4.6.g). Large unicellular hairs with a non-exserted basal cell occur on the abaxial midrib in conjunction with thinly cutinised, curly paired and unpaired hairs (Fig. 4.6.g).

4.3.3 Extant Morphology of Adult *Codia* Leaves

All species examined have simple leaves with entire margins and brochidodromous secondary venation (Fig. 4.6.h), incomplete areolation and veinlets with terminal idioblasts (Fig. 4.6.i) homologous to those in juvenile leaves (cf. Fig. 4.6.a). The adult leaves of at least two species, *C. albifrons* and *C. discolor*, possess stomata with a cutin ledge and paired hair bases in the areoles (e.g. Fig. 4.6.j). The subsidiary cells in adult leaves that have a cutin ledge or ring are anisocytic, being arranged in a very narrow band around the guard cells (Fig. 4.6.k) while other species are anomocytic. No adult leaves have a t-piece at the stomatal pole. *Codia nitida* leaves lack paired hairs and a stomatal cutin ledge (Fig. 4.6.l) while *C. montana* has a stomatal cutin ledge, lacks paired hair bases but has prominent and crystalline epicuticular wax (Fig. 4.6.m). The adaxial surface of all species is characterised by star-like configurations where an enlarged central cell is surrounded by 5-9 epidermal cells (Fig. 4.6.n) with corner thickenings in some species, probably due to the presence of a mucilaginous hypodermis (Dickison 1975*b*).

4.3.4 Comparison of *Callicoma* and Juvenile *Codia* Leaves

Callicoma serratifolia can be distinguished from all other Cunoniaceae genera on combined leaf morphology and cuticle characters (Table 4.3). Diagnostic features include craspedodromous secondary venation for the length of the leaf, percurrent tertiary venation, a prominent sinus formed by tertiary veins, imperfect areolation, a wavy cutin frill surrounding anomocytic stomata without t-pieces, small paired hair bases and large unicellular hairs with no basal cell and a ribbed abaxial midrib with slightly exserted hair bases.

Carpenter and Buchanan (1993) have previously reported the presence of a stomatal cutin frill and small paired hair bases in *C. serratifolia*, a feature shared with the adult leaves of at least two species of *Codia, C. albifrons* and *C. discolor.* Morphologically, extant adult *Codia* foliage differs from that of *C. serratifolia* by the presence of brochidodromous venation and entire leaf margins. However, the juvenile foliage of at least one *Codia* species is superficially similar to that of *C. serratifolia* but differs by the presence of apically curved basal veins, a t-piece at each stomatal pole, a weak anisocytic subsidiary cell arrangement and a cutin ring or ledge rather than a wavy frill. Juvenile *Codia* leaves at some developmental stage may be entirely serrate but these were not present on the single specimen examined. Secondary veins in *Callicoma* are never basally deflected near the sinus (Fig. 4.2.b) whereas these deflections occur in the juvenile leaves of *Codia* (Fig. 4.5.a), in addition to tubular terminal idioblasts on veinlets which is a feature considered diagnostic for the genus by Rao and Dickison (1985*b*).

4.3.5 *Callicoma serratifolia* Macrofossils

4.3.5.1 Little Rapid River, north-western Tasmania

The leaves and leaf fragments have strong craspedodromous secondary venation and prominent single serrations with mucronate-glandular apices (Fig. 4.7.a-c) for the length of the leaf (Fig. 4.7.c). In several leaves, secondary veins bifurcate near the midrib and terminate at adjacent teeth (Fig. 4.7.c), which occasionally occurs in *C. serratifolia* (see Fig. 4.3.a). Tertiary venation is weakly percurrent with veins from adjacent secondaries converging at a sinus to produce a small gland (Fig. 4.7.a). The higher order veins are random reticulate with imperfect areolation (Fig. 4.7.d). A

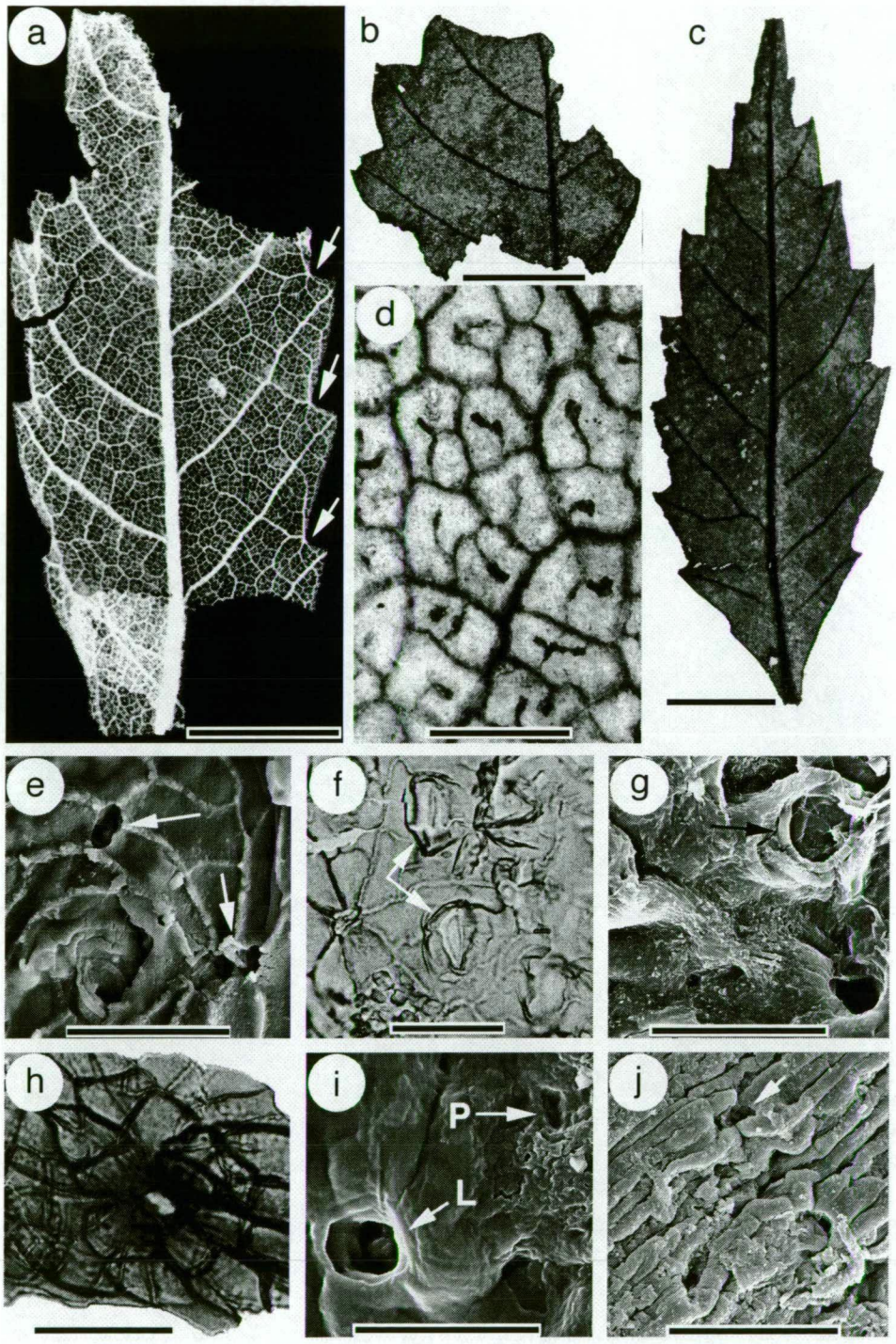
Table 4.3. Morphological features typical of *Callicoma serratifolia* that are useful in identifying leaf and infructescence macrofossils

Feature/structure	Description
Leaves and venation	Simple; craspedodromous straight secondary veins; percurrent tertiary veins. Secondary veins not basally deflected near sinus.
Leaf margin	Entirely serrate; commonly single, mucro-glandular apex.
Sinus	Prominent, formed by the convergence of tertiary veins.
Areolation/veinlets	Imperfect. Areoles pentagonal to quadrangular. Veinlets linear or once branched, sheath absent. Square terminal idioblasts ± present.
Adaxial surface	Epidermal cells isodiametric to round, smooth, non-sinuous. Large unicellular hairs common on veins and midrib.
Abaxial surface	Stomata with a cutin frill and an anomocytic subsidiary cell arrangement, arranged in areoles with small paired hair bases. Epidermal cells isodiametric to round, non-sinuous. Large unicellular hairs present on veins and midrib.
Hair bases	Simple, no basal cell, 5-7 radially modified epidermal cells.
Abaxial midrib	Venal cells elongated, ribbed, simple hair bases slightly exserted.
Infructescence	Ball infructescence, superior 2(-3) carpellate ovary, dehiscent by inner ledge, no vascular connective. Petals absent. Sepals 4-6, unicellular and paired hairs present. Stomata with a cutin frill and an anomocytic subsidiary cell arrangement. Seeds round, reticulate and tuberculate-papillate surface.

Figs 4.7.a-j. Mummified leaves and leaf fragments and cuticle of fossil *Callicoma serratifolia* from Little Rapid River, north-western Tasmania.

Fig. 4.7.a. Cleared leaf (LRR1-1648) showing craspedodromous secondary venation and sinuses (arrows). Scale bar = 10 mm.
Fig. 4.7.b. Leaf fragment (LRR1-3002). Scale bar = 10 mm.
Fig. 4.7.c. Whole leaf (LRR1-3005). Scale bar = 5 mm.
Fig. 4.7.d. Light micrograph showing imperfect areolation and the presence of square terminal idioblasts in specimen LRR1-1648. Scale bar = 500 μm.

Figs 4.7.e-j. Light and scanning electron micrographs of the cuticle of LRR1-1648.
Fig. 4.7.e. Inner abaxial surface showing anomocytic stomata and small paired hair bases (arrows). Scale bar 25 μm.
Fig. 4.7.f. Abaxial cuticle showing stomatal cutin frill (arrows) and paired hair bases. Scale bar = 25 μm.
Fig. 4.7.g. Outer abaxial surface showing stomatal cutin frill (arrow). Scale bar = 25 μm.
Fig. 4.7.h. Unicellular hair base on vein showing five radial epidermal cells with no basal cell. Scale bar = 30 μm.
Fig. 4.7.i. Large unicellular hair base (L) on abaxial veins with small paired hair bases (P) in adjacent areole. Scale bar = 20 μm.
Fig. 4.7.j. Abaxial midrib showing raised and elongated venal cells and large unicellular hair bases (arrow). Scale bar = 40 μm.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sheath is absent or not preserved on the veinlet endings with square terminal idioblasts variable in abundance (Fig. 4.7.d). The subsidiary cell arrangement is anomocytic with stomata that have a prominent frill of cutin associated with small paired hair bases in the areoles (Fig. 4.7.e-g). Large unicellular hair bases are simple with radially modified basal epidermal cells without a foot cell and occur on adaxial and abaxial surfaces over veins (Figs 4.7.h-i) and on the abaxial midrib. The midrib venal cells are elongated, rectangular, non-sinuous and raised, giving a ribbed appearance (Fig. 4.7.j). The leaves described here differ from those of juvenile *Codia* in morphology (e.g. the absence of brochidodromous venation, tubular terminal idioblasts, anisocytic stomata with t-pieces and the presence of a ribbed abaxial midrib with exserted hair bases) but are indistinguishable from extant *C. serratifolia* and so are assigned to that species.

The ball infructescences (Fig. 4.8.a-b) are superficially similar to those present in *Callicoma, Pancheria* and *Codia.* These genera form Engler's (1928) tribe Pancherieae which is characterised by the occurrence of flowers in spherical heads. The infructescence examined in detail consists of approximately 20-25 individual fruits in a compact spherical head c. 20 mm in diameter (Fig. 4.8.b). The peduncle is short, c. 5 mm long (Fig. 4.8.b), and is probably not preserved in its entirety. A long peduncle is preserved in specimen LRR1-4054 (Fig. 4.8.a). Individual fruits are formed by a superior bicarpellate ovary that is ventrally dehiscent along the inner ledge without a vascular connective (Fig. 4.8.c). Sepals are c. 2 mm long and c. 1 mm wide (Fig. 4.8.c) and are covered in both unicellular and paired hair bases (Fig. 4.8.d-f) and stomata with a cutin frill (Fig. 4.8.g) identical to that found on the leaves (Fig. 4.4.c) and sepals (Fig. 4.5.c) of extant *C. serratifolia.* Petals and a nectary disk are either absent or are not preserved. The fruits can be distinguished from those of *Codia,* which are indehiscent and semi-inferior, and *Pancheria* where the sepals are scarcely pubescent with unicellular hairs only. Seed coats could not be located within the dehisced fossil carpels. On the basis of floral structure and hair and stomatal features the fossil can be assigned to extant *C. serratifolia.* A close relationship can be inferred between the leaves and infructescences despite the lack of organic connection.

4.3.5.2 Berwick Quarry, Victoria

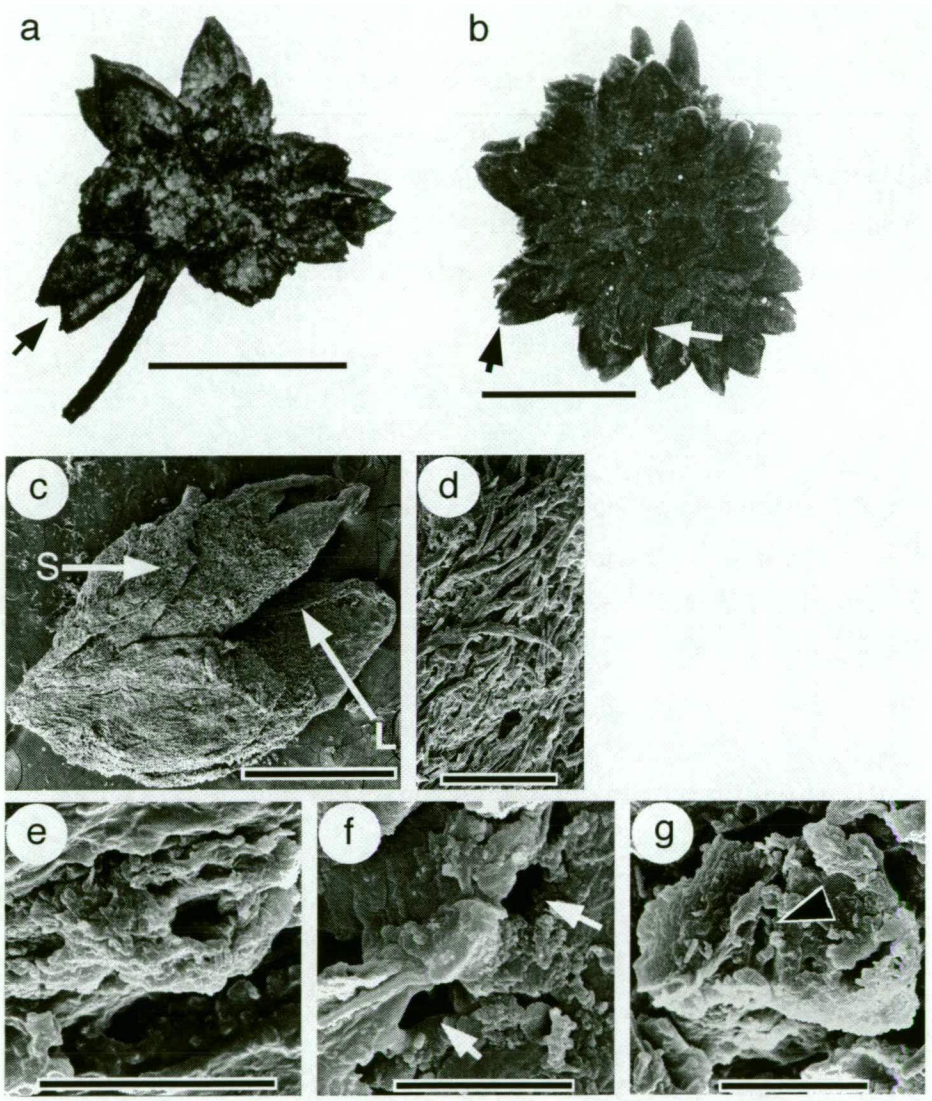
The two specimens (SB-220 and 319) considered by Pole *et al.* (1993) to have affinities with *Callicoma* have regularly serrate, mucronate margins, craspedodromous secondary venation and a sinus formed by tertiary vein convergence (Fig. 4.9.a-b). Tertiary veins are poorly preserved but appear to be weakly percurrent in specimen

Fig. 4.8.a-g. Fossil reproductive structures of *Callicoma serratifolia* from Little Rapid River, north-western Tasmania.

Fig. 4.8.a-b. Whole mummified fossil infructescences. Scale bar for both = 10 mm.
Fig. 4.8.a. LRR1-4054. Note the long peduncle and prominent bicarpellate fruit that has dehisced (arrow).
Fig. 4.8.b. LRR1-3015. Note short peduncle (white arrow) and slightly exserted, ventrally dehiscent carpels (black arrow).

Fig. 4.8.c. Single flower removed from the specimen LRR1-3015. Carpels are dehisced by inner ledge (L) and surrounded by 4-5 sepals (S). One carpel is ventrally split. Scale bar = 1 mm.

Figs 4.8.d-g. Scanning electron micrographs of the sepal surface of specimen LRR1-3015.
Fig. 4.8.d. Preserved hairs. Scale bar = 100 μm.
Fig. 4.8.e. Large unicellular, exserted hair bases with no basal cell. Scale bar = 20 μm.
Fig. 4.8.f. Small paired hair bases (arrows). Scale bar = 10 μm.
Fig. 4.8.g. Stoma with poorly preserved cutin frill. Note vertical stomatal pore in centre (arrow). Scale bar = 15 μm.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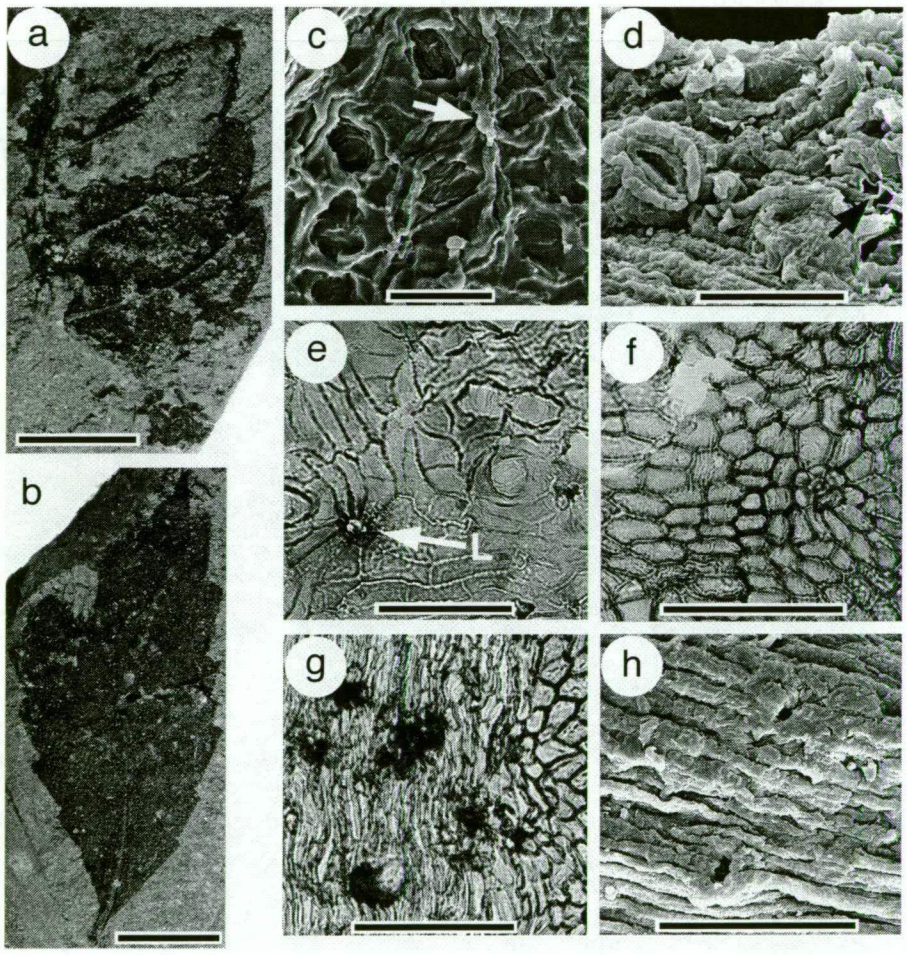
Figs 4.9.a-h. Leaf compression fossils and cuticle of *Callicoma serratifolia* from Berwick Quarry, Victoria.

Figs 4.9.a-b. Leaf compression fossils. Scale bar for both = 10 mm.
Fig. 4.9.a. Incomplete leaf with serrate margin (SB-319).
Fig. 4.9.b. Lower portion of a leaf with petiole preserved.

Figs 4.9.c-d. Scanning electron micrographs of the cuticle of the abaxial surface of SB-319. Scale bar for both = 30 μm.
Fig. 4.9.c. Inner surface showing stomata with an anomocytic subsidiary cell arrangement and small paired hair bases (arrow).
Fig. 4.9.d. Outer surface showing well preserved stomatal cutin frill and small paired hair bases (arrow).

Figs 4.9.e-g. Light micrographs of specimen SB-319.
Fig. 4.9.e. Abaxial cuticle showing stomata in areoles and elongated, non-sinuous venal cells. Large, simple unicellular hair bases (L) are common on major veins. Scale bar = 50 μm.
Fig. 4.9.f. Adaxial cuticle showing isodiametric epidermal cells with large unicellular hair bases on veins. Hair bases are simple with no foot cell. Scale bar = 100 μm.
Fig. 4.9.g. Adaxial midrib showing elongated venal cells and slightly raised hair bases. Scale bar = 100 μm.

Fig. 4.9.h. Scanning electron micrograph of the outer abaxial midrib showing elongated, raised venal cells and large unicellular hair bases with no foot cell. Scale bar = 50 μm.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SB-319 (Fig. 4.9.a), with several converging at a sinus. Subsidiary cell arrangement is of the anomocytic type (Fig. 4.9.c) and stomata have a prominent, well preserved cutin frill (Fig. 4.9.d) and are associated with small paired hair bases in areoles (Fig. 4.9.c-e). Large unicellular hair bases without basal cells, identical to those in extant *C. serratifolia*, are present on the lower order veins (Fig. 4.9.e cf. Fig. 4.4.a). Adaxial epidermal cells are isodiametric to round with unicellular hair bases surrounded by 5-6 radially modified epidermal cells with no basal cell (Fig. 4.9.f) and are also common on the adaxial midrib (Fig. 4.9.g). The abaxial midrib is covered in slightly exserted unicellular hair bases between raised and elongated venal cells (Fig. 4.9.h). The fossils described here conform to the features considered characteristic of extant *C. serratifolia* leaves and so are assigned to that species.

A third specimen (Fig. 4.10.a; SB-315) considered by Pole *et al.* (1993) to have affinities with *Callicoma* has craspedodromous secondary venation, weak percurrent tertiary veins which form a sinus (Fig. 4.10.a), an anomocytic subsidiary cell arrangement (Fig. 4.10.b), stomata without t-pieces (Fig. 4.10.b), adaxial isodiametric epidermal cells with elongated venal cells and large unicellular hair bases with radially modified epidermal cells but without a basal cell (Fig. 4.10.c). The abaxial midrib is covered in unicellular hair bases between elongated and raised venal cells (Fig. 4.10.d). Based on the secondary venation type, the presence of a sinus and hair bases with radially arranged epidermal cells and exserted hair bases on the abaxial midrib, the fossil has affinity with Cunoniaceae, and in particular *Callicoma*. However, the absence of both a stomatal cutin frill and small paired hair bases combined with the distinctly ornamented abaxial surface and slightly sunken stomata (Fig. 4.10.e) distinguishes the fossil from extant *Callicoma*. Most Cunoniaceae genera have a sinus formed by the convergence of tertiary veins but only *Acrophyllum* and some *Weinmannia* species have deeply serrate leaves with mucronate apices similar to the fossil. However, *Acrophyllum* has strongly sinusoidal adaxial epidermal cells and of c. 50 species of *Weinmannia* examined none have been found that conform to the fossil. The affinities of this fossil are as yet unresolved, but it is not a leaf of extant *C. serratifolia*.

4.3.5.3 Stuart Creek (Eyre Formation), South Australia

The majority of the 'Serrate-coarse' fossils described by Greenwood *et al.* (1990) at the Stuart Creek locality occur on large slabs of rock which were formed by the silicification of leaf mats (Fig. 4.11.a). Although some of the specimens are collectable, the majority remain *in situ* due to collection and transportation problems.

Figs 4.10.a-e. ?Cunoniaceae gen. et sp. indet. (SB-315) from Berwick Quarry, Victoria.

Fig. 4.10.a. Compression leaf macrofossil. Scale bar = 10 mm.

Fig. 4.10.b. Light micrograph of the abaxial cuticle showing stomata with an anomocytic subsidiary cell arrangement and an inner stomatal ledge. Scale bar = 20 μm.

Fig. 4.10.c. Light micrograph of the adaxial cuticle. Scale bar = 100 μm.

Fig. 4.10.d. Scanning electron micrograph of the outer surface of the abaxial midrib showing ribbed venal cells and unicellular hair bases. Scale bar = 50 μm.

Fig. 4.10.e. Scanning electron micrograph of the outer cuticle of the abaxial surface showing slightly sunken stomata. Scale bar = 50 μm.

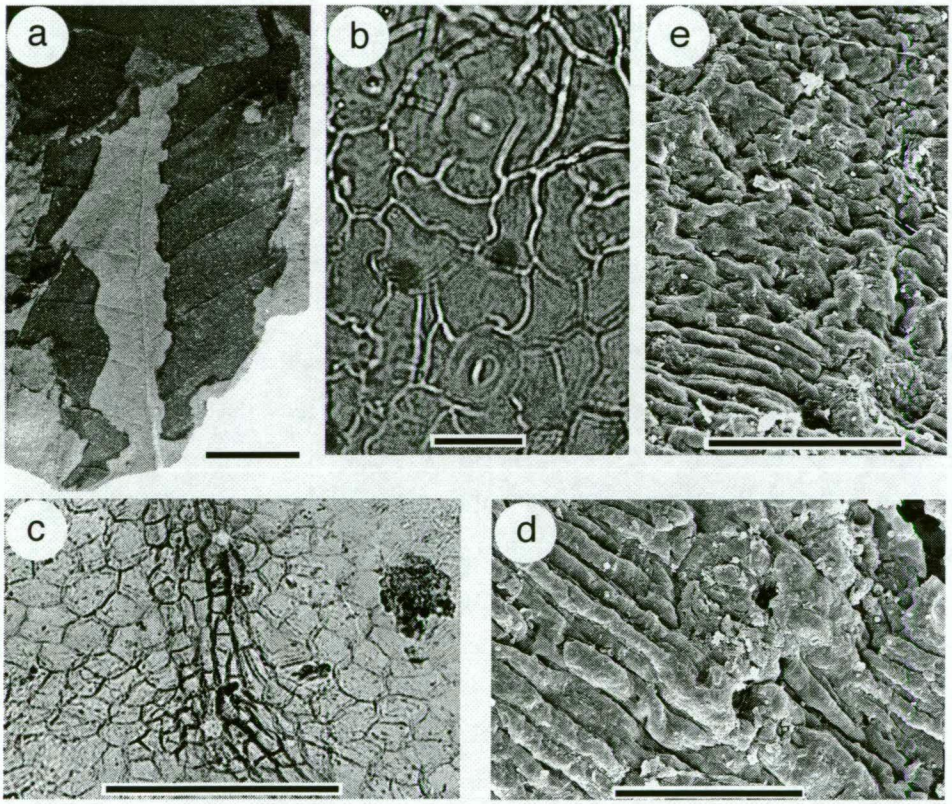
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Fig. 4.11.a. Section of a silcrete leaf mat from Stuart Creek, South Australia, showing a single incomplete leaf impression fossil of *Callicoma serratifolia* (arrow) associated with other unidentified angiosperm leaves. Scale bar = 50 mm.

Fig. 4.11.b. *In situ* leaf impression of fossil *C. serratifolia.* Note the prominent craspedodromous secondary veins that terminate at serrations. Scale bar = 10 mm.

Fig. 4.11.c. Leaf impression of fossil *C. serratifolia* (R364695) from Stuart Creek. Scale bar = 10 mm.

Figs 4.11.d-g. Photographs of a latex mould taken from a leaf impression of fossil *C. serratifolia* (specimen Fossil Leaf Type No. 3) from Stuart Creek. Scale bar for both = 10 mm.

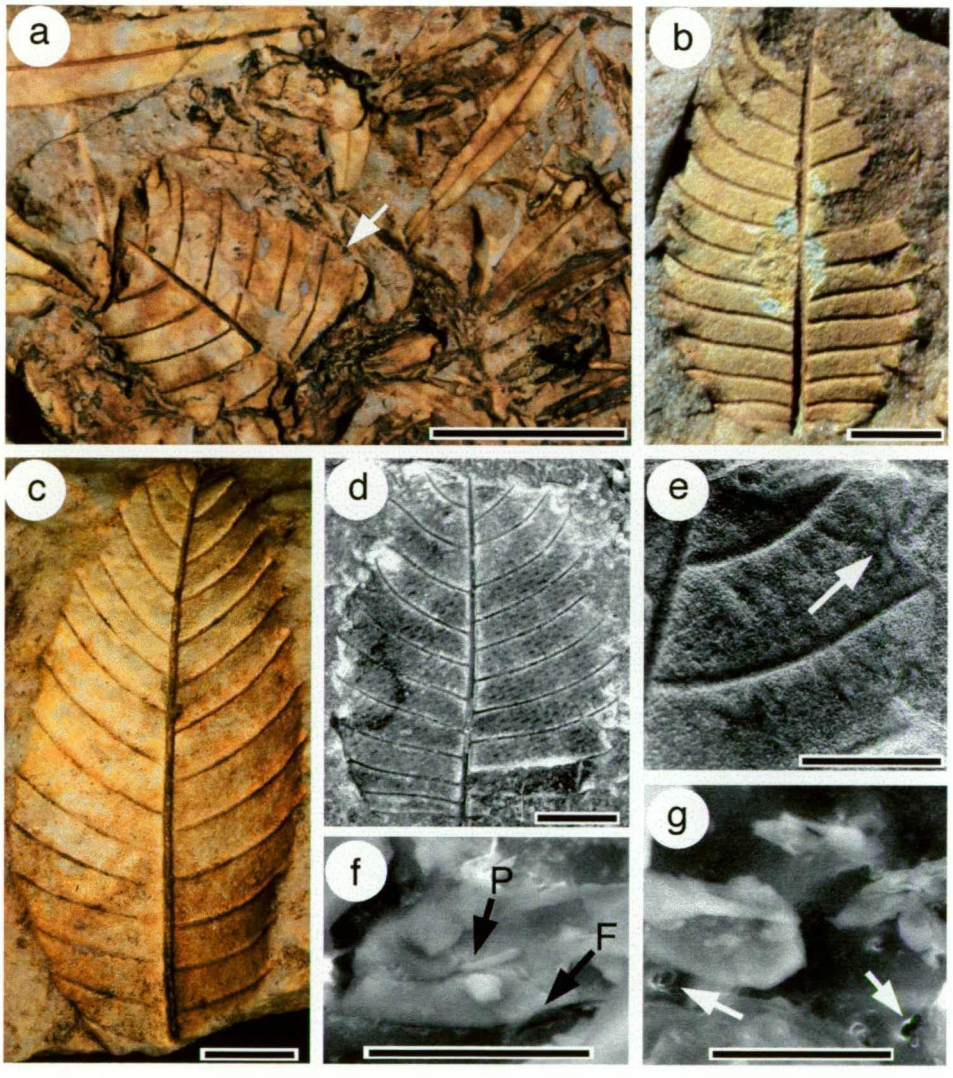
Fig. 4.11.d. Whole specimen.

Fig. 4.11.e. Photograph showing the convergence of tertiary veins at a sinus (arrow).

Figs. 4.11.f-g. Scanning electron micrographs of the outer abaxial surface of specimen Fossil Leaf Type No. 3. Scale bar for both = 20 μm.

Fig. 4.11.f. Collapsed stoma showing folded cutin frill (F). Note the closed stomatal pore (P).

Fig. 4.11.g. Small paired hair bases (arrows) between poorly preserved stomata.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With the exception of *Eucalyptus*, the 'Serrate-coarse' fossil type is one of the most recognisable leaf fossils that occurs at the locality, with distinctive craspedodromous secondary venation and serrate leaf margins (Fig. 4.11.a-b).

The two specimens (Fig. 4.11.c-d) collected and examined are both poorly preserved; one is an impression of a leaf in a small rock that was collected and the other is a latex mould of a specimen taken in the field. The leaf impression (Fig. 4.11.c; R364695) lacks surface detail but has craspedodromous secondary venation and weak percurrent tertiary veins that are identical to extant *Callicoma* (Fig. 4.11.c cf. Fig. 4.3.b). Assignment to *Callicoma* is tentative in the absence of any surface or cuticle preservation. The latex mould taken from an *in situ* leaf impression (Fig. 4.10.d) exhibits differential surface preservation. Secondary venation is craspedodromous with prominent, regular single serrations. Tertiary venation is weakly percurrent with several veins converging at a sinus (Fig. 4.11.e). Stomata are very poorly preserved with a folded cutin frill (Fig. 4.11.f) and are associated with small paired hair bases (Fig. 4.11.g). Large unicellular hairs bases are also present on the midrib but are poorly preserved with no epidermal cell definition. The latex mould specimen described here can be assigned to extant *C. serratifolia* with confidence on the basis of leaf, stomatal and hair morphology. Although no other specimens in the field or the laboratory had their surface structure examined, it is reasonable to also assign all those specimens with a similar venation pattern to the latex specimen to *C. serratifolia.*

4.3.5.4 Lemonthyme Creek core, north-western Tasmania

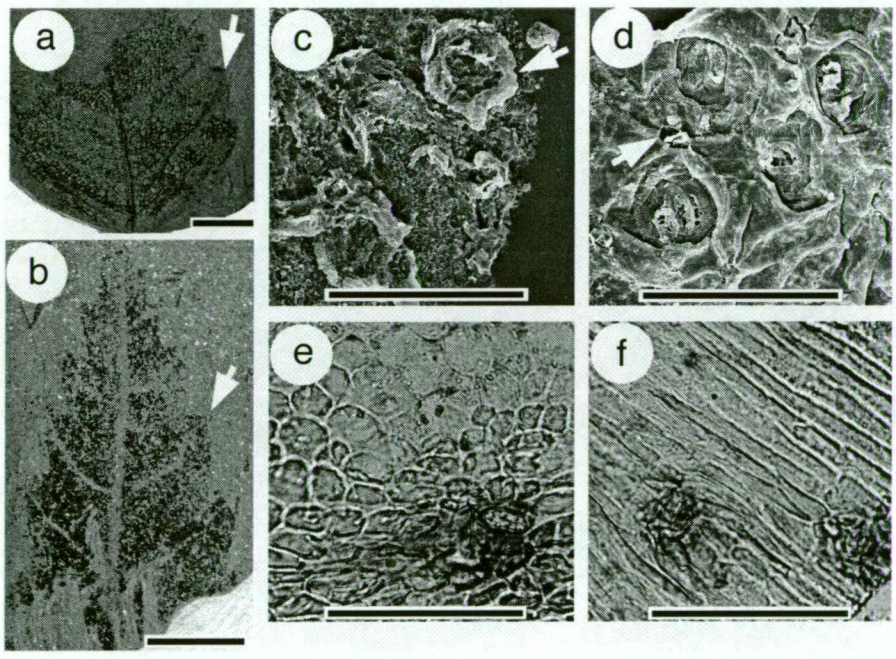
One specimen (Fig. 4.12.a; LT-67 and counterpart) is a mid-lamina region of a large leaf so the apex, base and petiole are absent. Another specimen (Fig. 4.12.b; LT-1000) has an acute leaf apex preserved identical to that present in some leaves of extant *C. serratifolia* (e.g. Fig. 4.3.a). The leaf margin in both fossils is prominently serrate due to the craspedodromous secondary venation. Tertiary veins are poorly preserved in both specimens but a sinus is discernible on one specimen, LT-1000 (Fig. 4.12.b). The stomata have a prominent cutin frill (Fig. 4.12.c), occur in areoles along with small paired hair bases and have an anomocytic subsidiary cell arrangement (Fig. 4.12.d). Adaxial epidermal cells are isodiametric in shape (Fig. 4.12.e) with venal cells elongated and slightly raised in outline. Large, unicellular simple hair bases are common on the abaxial midrib (Fig. 4.12.f). The absence of stomatal t-pieces and hair bases with a basal cell and the presence of a ribbed abaxial midrib with prominently exserted hair bases distinguishes the fossil leaves from those of juvenile *Codia.* The fossil leaves could not be distinguished from the leaves of extant *C. serratifolia* so are

Figs 4.12.a-b. Leaf compressions and cuticle of fossil *Callicoma serratifolia* from the Lemonthyme Creek core, north-western Tasmania.

Figs 4.12.a-b. Leaf compressions.
Fig. 4.12.a. Mid-lamina and margin of specimen LT-67. Arrow indicates a mucronate tooth apex. Scale bar = 10 mm.
Fig. 4.12.b. Acuminate leaf apex of specimen LT-1000 showing prominent marginal serrations (arrow) and craspedodromous secondary venation. Scale bar = 10 mm.

Figs 4.12.c-d. Scanning electron micrographs of the abaxial cuticle of specimen LT-67.
Fig. 4.12.c. Outer surface showing stomata with a cutin frill (arrow).
Fig. 4.12.d. Inner surface showing small paired hair bases (arrow) between anomocytic stomata. Scale bar = 30 μm.

Figs 4.12.e-f. Light micrographs of specimen LT-67. Scale bar for both = 50 μm.
Fig. 4.12.e. Adaxial surface. Note large unicellular hair base (lower right) with no basal cell.
Fig. 4.12.f. Abaxial midrib showing ribbed venal cells and unicellular hair bases.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assigned to that species.

4.3.5.5 Cethana, north-central Tasmania

The assignment of the leaf macrofossil to *C. serratifolia* by Carpenter and Buchanan (1993) is considered valid here based on morphological (craspedodromous secondary venation) and cuticular characters (stomatal cutin frill, anomocytic subsidiary cell arrangement and paired hair bases). A single specimen is illustrated and referred to by Carpenter and Buchanan (1993), however during this study an additional four leaf macrofossils of the species were located (Fig. 4.13.a-e). The secondary venation in all the specimens is craspedodromous (c.f. Fig. 4.13.a-c) and the tertiary veins are weakly percurrent (Fig. 4.12.e). A single specimen has a cuneate leaf base and petiole preserved (Fig. 4.13.b) whilst another specimen has an acuminate leaf apex (Fig. 4.13.e). The shape of the leaf base and apex were not preserved in the specimen examined by Carpenter and Buchanan (1993). These features, preserved on the specimens presented here, are all consistent with the extant species and so provide further support for this identification.

Assignment of the infructescence to extant *C. serratifolia* is also considered valid here based on fruits clustered into a globose head that contain tuberculate seed coats. Carpenter and Buchanan (1993) noted that, despite the absence of any organic connection, a relationship between leaf and infructescence is highly likely. This is supported by the inability to distinguish either structure, vegetative or reproductive, from those of extant *C. serratifolia.*

4.3.5.6 Vegetable Creek, New South Wales

The leaf impression fossil of *Callicoma primaeva* (Fig. 4.14.a) was considered by Ettingshausen (1888) to have affinities with extant *C. serratifolia* and extinct *C. pannonica* from the Tertiary flora of the Eperies, Austro-Hungary (Unger 1866; see below) based on the craspedodromous secondary venation pattern, percurrent tertiary veins and marginal serrations. The erection of a new fossil species by Ettingshausen (1888) for the Vegetable Creek fossil is perhaps unwarranted considering the strong similarities of the macrofossil to extant *C. serratifolia*, however assignment to this species is premature without examining the cuticular morphology of the holotype which has not been successfully located.

Figs 4.13.a-e. Leaf macrofossils of *Callicoma serratifolia* from Cethana, north-central Tasmania. Scale bar for all = 10 mm.

Fig. 4.13.a. Specimen C-1022. Note craspedodromous secondary veins that terminate at mucronate tooth apices (arrow).

Figs 4.13.b-c. Specimen C-1017.
Fig. 4.13.b. Whole macrofossil.
Fig. 4.13.c. High magnification of the leaf margin showing craspedodromous venation and weakly percurrent tertiary veins.

Fig. 4.13.d. Incomplete and poorly preserved small leaf (specimen C-1020).

Fig. 4.13.e. Leaf apex (specimen C-1021).

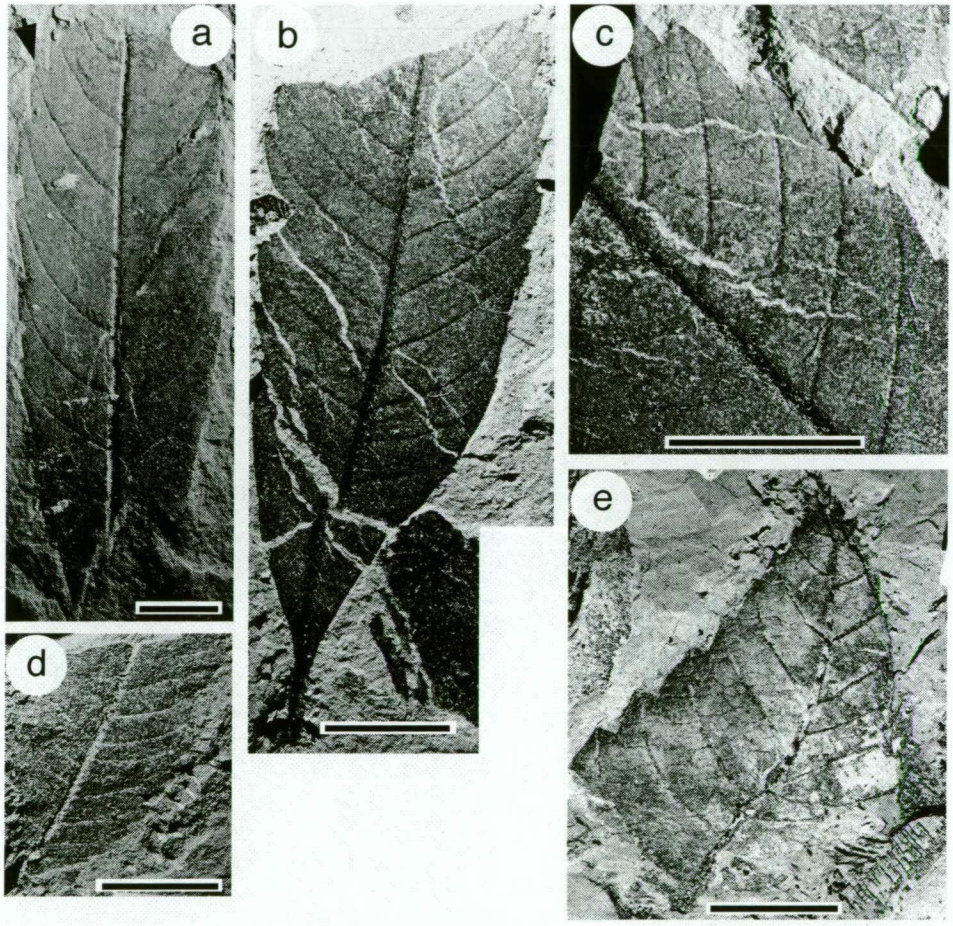
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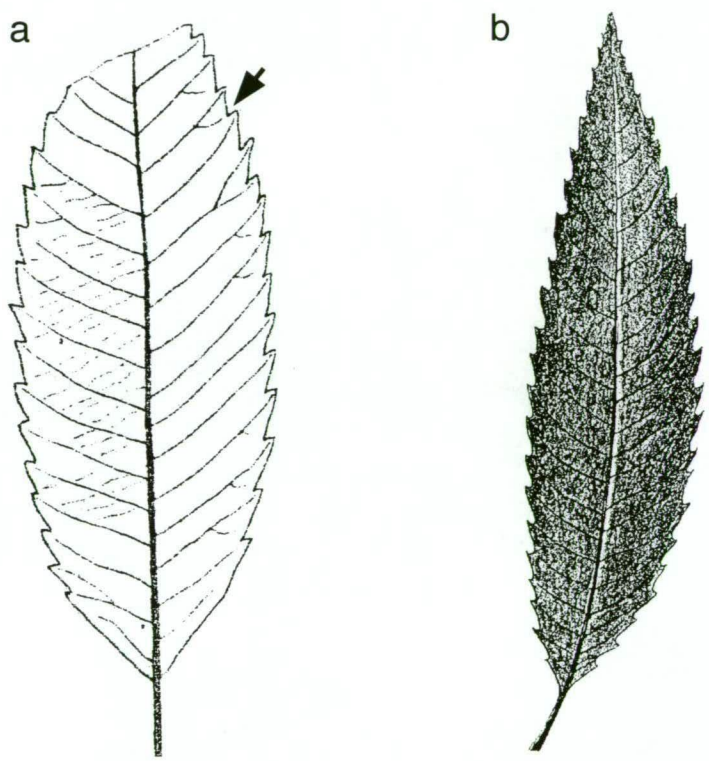
Fig. 4.14.a. Line drawing of fossil *Callicoma primaeva*. Ettingshausen (1888) described this species from Vegetable Creek, New South Wales. The drawing is taken from Ettingshausen (1888) as the original specimen could not be located. The drawing illustrates a craspedodromous secondary venation pattern and the presence of a sinus formed by the convergence of tertiary veins (arrow).

Fig. 4.14.b. Line drawing of fossil *Callicoma pannonica* from Tertiary sediments in the Eperies, Austro-Hungary, Europe. The drawing is taken from Unger (1866) as the original specimen could not be located.


a
b

4.3.5.7 Eperies, Austro-Hungary, Europe

Although the illustration of *Callicoma pannonica* (Fig. 4.14.b) by Unger (1866) superficially looks like those leaves of extant *Callicoma*, the description lacks any detail of diagnostic features to enable confident assignment to this taxon. Furthermore, it is extremely likely that the assignment of the fossil to *Callicoma* is a misidentification simply based on the distribution of the extant genus, and it is considered here to be inappropriately assigned to the genus *Callicoma*. The fossil has been reassigned elsewhere to *Platanus* (see Mai 1995).

4.3.6 *Codia* Macrofossils

4.3.6.1 West Dale, south-western Western Australia

The macrofossil is incomplete, lanceolate, c. 50 mm long and 18 mm at the widest point with an acute base (Fig. 4.15.a). The petiole and leaf apex are not preserved. The secondary venation is predominantly craspedodromous with regular, single serrations the length of the leaf. Tertiary venation is not clearly visible but appears to be weakly percurrent (Fig. 4.15.b). Weak sinuses are present in the upper portion of the leaf (Fig. 4.15.b) but are absent or very weak in the lower portion of the leaf as each secondary vein bifurcates near the sinus with one vein basally deflected, terminating at the tooth, while the other vein terminates at the sinus or more commonly joins to another vein from the adjacent secondary vein (see Fig. 4.15.c). This is considered homologous to the tooth vascularisation in juvenile *Codia* foliage (Fig. 4.15.d). Basal secondary veins are prominently curved apically at a 50-60° angle and terminate at small teeth which are identical to those in juvenile *Codia* (Fig. 4.15.a cf. Fig. 4.6.a).

Areoles are weakly defined (Fig. 4.15.e) with sections of the abaxial surface showing the outline of epidermal cells and the subsidiary cell arrangement, which appears anisocytic. Stomata are surrounded by a raised ledge or ring and are associated with paired hair bases (Fig. 4.15.f-g). Minor veins are covered in small, paired and unpaired hairs with the remnants of a basal cell (Fig. 4.15.g). Abaxial midrib cells are elongated, non-sinuous and are not raised (Fig. 4.15.e). Large unicellular hair bases with non-exserted basal cells are present in conjunction with small paired and unpaired hairs on the abaxial midrib (Fig. 4.15.h-i). The adaxial epidermal cells are often arranged in star-like configurations where cells are radially arranged around a central

Figs 4.15.a-c, e-j. *Codia australiensis* from West Dale, south-western Western Australia.

Fig. 4.15.a. Incomplete macrofossil showing serrations (arrow). Scale bar = 5 mm.

Fig. 4.15.b. Higher magnification of the upper teeth. Note sinus (arrow). Scale bar = 5 mm.

Fig. 4.15.c. Secondary vein bifurcating near the sinus of a tooth in the lower leaf; one vein terminates at the tooth (V), the other loops within the leaf margin (S). A vein originates from the loop and terminates at the sinus. Scale bar = 5 mm.

Fig. 4.15.d. Sinus of an extant juvenile *Codia* leaf showing secondary vein bifurcating near sinus of basal tooth; one vein terminates at tooth (V), the other loops within the leaf margin (S). A vein originates from the loop and terminates at the sinus. Scale bar = 5 mm.

Figs 4.15.e-i. Scanning electron micrographs of the outer abaxial surface and midrib of *C. australiensis.*

Fig. 4.15.e. Midrib and lamina. Scale bar = 500 μm.

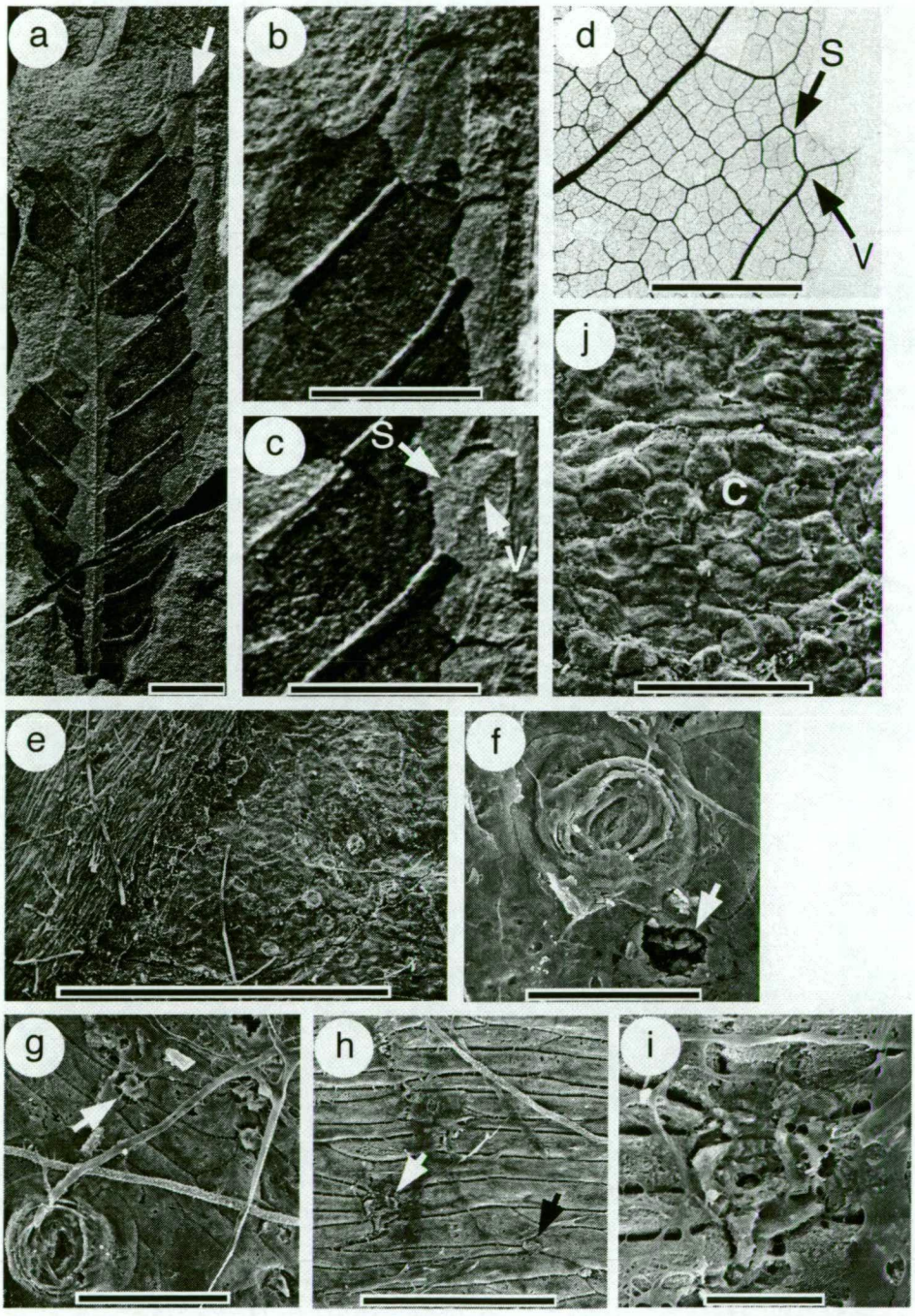
Fig. 4.15.f. Stoma with cutin frill near paired hair bases (arrow). Scale bar = 30 μm.

Fig. 4.15.g. Unicellular hair bases on minor veins (arrow). Scale bar = 30 μm.

Fig. 4.15.h. Midrib showing large (white arrow) and small (black arrow) unicellular hair bases. Scale bar = 100 μm.

Fig. 4.15.i. Large unicellular hair base on midrib. Scale bar = 15 μm.

Fig. 4.15.j. Scanning electron micrograph of the outer adaxial surface. Note an enlarged central cell (C) surrounded by radially arranged epidermal cells. Scale bar = 100 μm.


a
b
c
S
V
d
S
V
j
C
e
f
g
h
i

cell (see Fig. 4.15.j).

The specimen described here conforms to several features typical of *C. serratifolia* (e.g. craspedodromous secondary venation, a sinus formed by tertiary veins, cutin frill on stomata and paired hair bases), however the basal deflection of secondary veins near the sinus, anisocytic subsidiary cell arrangement, hair bases with a basal cell, the occurrence of apically directed basal secondary veins, small unpaired and paired hairs on the abaxial midrib, non-ribbed venal cells and non-exserted hair bases suggests an affinity to the juvenile leaves of at least one *Codia* species. Due to the type of preservation of the macrofossil, the inner surface was unavailable to determine the presence or absence of t-pieces at stomatal poles. The absence of basal brochidodromous venation distinguishes it from the juvenile foliage of *Codia* examined in this study. The fossil is assigned to the new species *Codia australiensis*.

4.3.6.2 Morwell Formation, Latrobe Valley, Victoria

The dispersed cuticle described by Blackburn (1985) does not have any cuticular features considered diagnostic of *Callicoma* (see Table 4.3). Instead, the cuticle has features more typical of some *Codia* species which include an anisocytic subsidiary cell arrangement, small guard cells (15-20 μm), simple hair bases with a basal cell and adaxial epidermal cells arranged in a rosette configuration over areoles. The sunken appearance of the stomata below the leaf surface, as described by Blackburn (1985), is possibly due to the presence of a cutin ledge. Although several features of the cuticle do conform to extant *Codia*, assignment to this or any other Cunoniaceae genus is premature without examination of the cuticle by scanning electron microscopy.

4.4 Systematics

The systematics of all the below mentioned fossils are detailed in Barnes and Hill (1999*b*, Appendix 1).

Callicoma Andrews

Callicoma serratifolia Andrews

Little Rapid River, north-western Tasmania

Reference leaf specimen: LRR1-1648.
Referred leaf specimens: LRR1-3000-3003, 3005-3009, 3013, 3016-3020.

Reference infructescence specimen: LRR1-3015.
Referred infructescence specimen: LRR1-4054.

Berwick Quarry, Victoria

1993 ?Cunoniaceae sp. '*Callicoma*' Pole *et al.*, p. 409, Fig. 38.

Reference specimen: SB-319.
Referred specimen: SB-220.

Stuart Creek, South Australia

Reference specimen: Latex mould of Fossil Leaf Type No. 3.
Referred specimen: R364695 (leaf surface lacks cuticular preservation, both specimens stored at Mineral Provinces Branch Biostratigraphy Section, Mines and Energy Resources, South Australia).

Lemonthyme Creek core, north-western Tasmania

Reference specimen: LT-67 and counterpart (LT-68).
Referred specimens: LT-162 and LT-1000.

Cethana, north-central Tasmania

Reference leaf specimen: C-480 (Carpenter and Buchanan 1993).
Referred leaf specimens: C-1017, 1020-1022.
Reference infructescence specimen: C-531 (Carpenter and Buchanan 1993).

Codia J.R.Forst. & G.Forst.

Codia australiensis R.W.Barnes & R.S.Hill, sp. nov. (Fig. 4.15.a-c, 4.15.e-j)

Diagnosis: Leaf small, simple and lanceolate, regularly serrate the length of the leaf.

Holotype: WAM P.88.84A (only specimen, housed in the Western Australian Museum, Perth).

Type locality: Darling Plateau, West Dale, 76 km east south-east of Perth and 325 km west south-west of Bevereley, Western Australia (32° 13.6' S, 116° 36.2' E; Hill & Merrifield 1993).

Etymology: Named to recognise the occurrence of *Codia* in Australia.

Description: The leaf is incomplete, lanceolate, c. 50 mm long and 18 mm at the widest point with an acute base (Fig. 4.15.a). The petiole and leaf apex are not preserved. The entire leaf margin is regularly serrate with serrations basally and apically convex in shape. The midrib and secondary veins are thick, pronounced and terminate at the teeth in the upper leaf (Fig. 4.15.b). The basal secondary veins are curved apically at a 50-60° angle and bifurcate near the sinus (Fig. 4.15.c), with a single basally deflected vein terminating at a small tooth and the other terminating at the sinus or within the leaf margin to adjacent secondary veins (Fig. 4.15.c). A sinus is present in the upper leaf at least and is formed by the tertiary veins which are weakly percurrent. Stomata occur in weak areoles (Fig. 4.15.e) with paired hair bases and have a collapsed ring of cutin (Fig. 4.15.f-g). Subsidiary cell arrangement appears to be anisocytic. Minor veins are covered in small paired and unpaired hairs (Fig. 4.15.g). The abaxial midrib venal cells are elongated, non-sinuous and not raised with large unicellular hair bases present in conjunction with small paired and unpaired hairs (Fig. 4.15.g-i). Small adaxial epidermal cells are radially arranged around an enlarged central cell (Fig. 4.15.j).

4.5 Discussion

4.5.1 Leaf Morphology of Extant *Callicoma serratifolia*

Callicoma serratifolia has a very distinctive leaf morphology compared to other genera in the Cunoniaceae and can be identified on combined leaf architecture and cuticular morphology (Table 4.3). Based on leaf architecture and cuticular features, *Callicoma serratifolia* appears to be homoblastic, which is quite unlike at least one species of *Codia* which is clearly heteroblastic.

The results of this study support several interpretations of Dickison (1975*b*) while contradict several of those of Kennedy and Prakash (1981). All leaves have simple craspedodromous secondary venation (also Dickison 1975*b*) and not cladodromous venation as reported by Kennedy and Prakash (1981). Cladodromous venation only occurs in leaves with entire margins where the secondary veins freely ramify towards the margin but never terminate at it (see Hickey 1979). Areolation is imperfect (see also Dickison 1975*b*) with areoles more or less pentagonal in shape. Kennedy and Prakash (1981) misinterpreted the classification of areolation patterns presented by Hickey (1979) which is divided into separate characters; development, arrangement, and shape and size. Kennedy and Prakash (1981) considered *C. serratifolia* to possess pentagonal areolation, which is the case for areole shape but not of the development, which is clearly imperfect (see Fig. 4.3.f-g).

Other gross morphological features used by Kennedy and Prakash (1981) to distinguish morphotypes are considered here to be too variable within a single plant or population of plants to be of any taxonomic use. For example, the number of serrations per secondary vein appears to be dependent on leaf growing conditions and size, where sun and small leaves have predominantly single serrations. Colleters are present at the base of the adaxial surface of the stipules in all specimens examined, and these tend to be shed with the stipules on the older foliage.

This study has confirmed the presence of two trichome types in *C. serratifolia* as identified by Dickison (1975*b*), Kennedy and Prakash (1981) and Carpenter and Buchanan (1993). Large, thick straight trichomes occur on the midrib and major veins, only rarely occurring on minor veins and areoles while smaller, thinly cutinised trichomes that are curly occur in association with the stomata, only sparsely occurring on minor veins. Kennedy and Prakash (1981) indicate that the Group A morphotype only has curly trichomes, however this study and that of Carpenter and Buchanan

(1993) clearly demonstrate that both types occur on all leaves but simply differ in their distribution, with the curly paired trichomes almost exclusively restricted to the areoles and smaller veins.

Based on the morphological data collected during this study and that presented by Dickison (1975*b*), the morphotypes of Kennedy and Prakash (1981) are not considered valid. A form with a rust coloured abaxial tomentum (also Harden 1990*a*), once described as *Callicoma ferruginea* D.Don. (see Bentham and Mueller 1864), that occurs in the Blue Mountains may warrant taxonomic recognition but requires further investigation.

4.5.2 Leaf Morphology of Extant *Codia* Species

The leaf morphology of *Codia* remains poorly studied, especially at the juvenile stage. However, it is apparent from both this study and the taxonomic key of Guillaumin (1948) that a distinctive juvenile phase is present in some *Codia* species. Serrate, often highly pubescent leaves present at some developmental stage may be a synapomorphy of Cunoniaceae, with independent evolution of entire margined leaves within several lineages, including *Codia. Pullea stutzeri* (Hyland and Whiffin 1993) and *Geissois benthamii* (Boland *et al.* 1985; R. W. Barnes pers. obs.) also possess serrate, highly tomentose juvenile foliage which is replaced by relatively glabrous and weakly serrate adult foliage.

Codia is a particularly interesting genus as it has a highly diverse cuticle and stomatal morphology. For example, at least two species, *C. discolor* and *C. albifrons*, possess stoma with a cutin ledge in association small paired hair bases. Other species may be highly glabrous or covered in a thick coating of wax, similar to that present in some *Pancheria* species (R. W. Barnes pers. obs.), which also predominantly occur in the maquis vegetation of New Caledonia (Specht 1981). Subsidiary cell arrangement is variable within the genus, with both the anisocytic and anomocytic types, as described by Dilcher (1974) and Baranova (1987), present. It is likely that cuticular characters would be useful to include in a phylogenetic analysis of the genus at the species level.

4.5.3 Macrofossils of *Callicoma serratifolia*

The misidentification of fossils as *C. serratifolia* can occur when the cuticular morphology or surface structures of all the specimens considered to represent a single fossil taxon is not examined (e.g. Pole *et al.* 1993). Important cuticular or leaf surface features include the presence of a cutin frill around each stoma and the presence of small paired trichome bases (see Table 4.3). For this reason, any records based solely on leaf shape, form and venation patterns (e.g. Unger 1866; Ettingshausen 1888) must be considered dubious at best. Therefore, these are excluded from any further discussion on the fossil record of the genus with all valid records presented in Table 4.4.

On combined gross morphological and cuticular characters, macrofossils from four localities (Little Rapid River, Lemonthyme Creek, Berwick Quarry and Stuart Creek) were assigned to extant *C. serratifolia.* In addition, the leaf and infructescence macrofossils described by Carpenter and Buchanan (1993) from Early Oligocene sediments at Cethana are also considered valid records of the extant species. This latter verification is based on the re-examination of the reference specimens and supplemented by more leaf macrofossils located during this study (see Fig. 4.12.a-e).

The single specimen from Berwick Quarry (SB-315; Fig. 4.9.a-e), assigned to ?Cunoniaceae sp. '*Callicoma*' by Pole *et al.* (1993), is not *C. serratifolia* but may represent another Cunoniaceae genus, possibly extinct. A formal identification of the specimen has not been made at this stage.

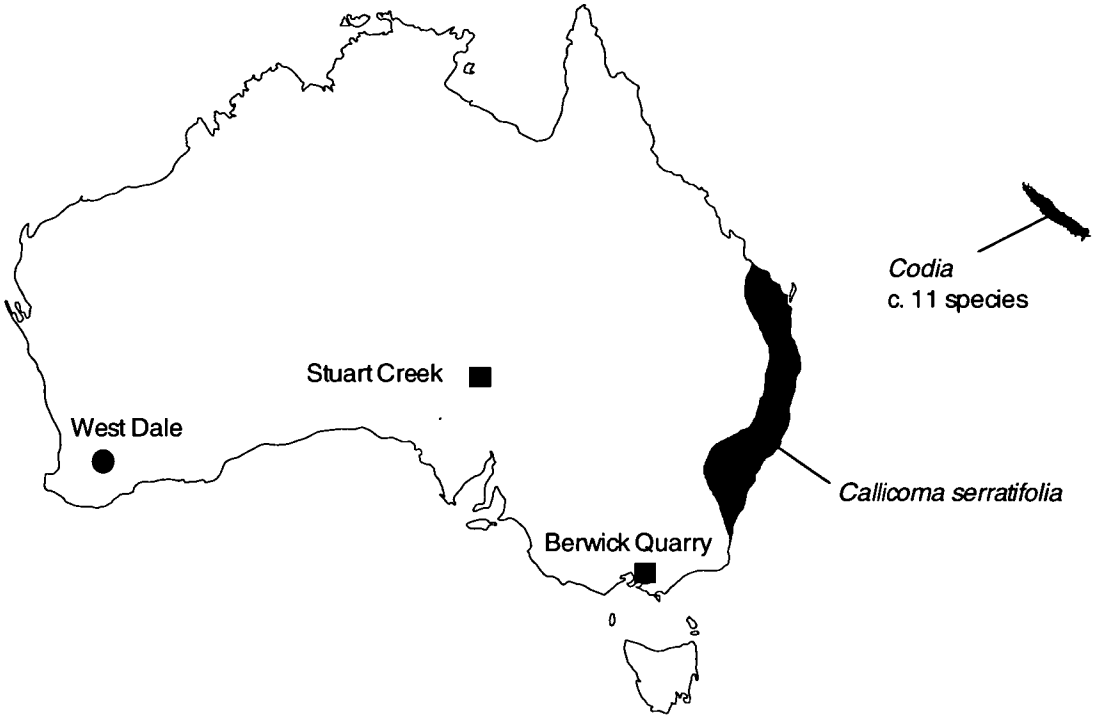
The Early Oligocene leaves (Cethana, Little Rapid River and Lemonthyme Creek core) and infructescences (Cethana and Little Rapid River) from Tasmania are the oldest fossils assignable to *C. serratifolia* (see Figs 4.16 and 4.17). However, as only a relatively small proportion of the total plant is represented by any of the macrofossils examined in this study, and there is no organic connection between those parts that are preserved, the fossil leaves and reproductive structures may equally represent the ancestor to extant *C. serratifolia* or, and more likely, one or more extinct relatives. Features that are identifiable in the extant species, such as phyllotaxy, growth habit, stipule morphology, wood anatomy, floral maturation pattern, and pollen morphology, are not preserved within the existing fossil record so comparisons of these features with the extant species cannot be made. However, as the fossils preserve a large quantity of data and they share many features of extant *Callicoma serratifolia* (Table 4.3) the assignment of the fossils in this study are considered to be justified.

Table 4.4. Verified and accepted macrofossil records of *Callicoma* and *Codia*

Source: [A] this study; [B] Carpenter and Buchanan 1993.

Taxon	Fossil type	Geological age	Fossil locality
Callicoma serratifolia [A]	Mummified leaves	Early Oligocene	Little Rapid River, north-western Tasmania
C. serratifolia [A]	Mummified infructescences	Early Oligocene	Little Rapid River, north-western Tasmania
C. serratifolia [A]	Leaf compressions	Early Oligocene	Lemonthyme Creek core, north-western Tasmania
C. serratifolia [AB]	Leaf compressions	Early Oligocene	Cethana, north-central Tasmania
C. serratifolia [B]	Infructescence compression	Early Oligocene	Cethana, north- central Tasmania
C. serratifolia [A]	Leaf compressions	Late Oligocene	Berwick Quarry, Victoria
C. serratifolia [A]	Leaf impressions in silcrete	Miocene to Pliocene	Stuart Creek, South Australia
Codia australiensis [A]	Mineralised, incomplete leaf	Middle Eocene-Oligocene	West Dale, Western Australia

Fig. 4.16. Map of Australia and New Caledonia showing the past (circles and squares) and present (shaded) distribution of *Callicoma serratifolia* and *Codia* species. A single macrofossil of *Codia, C. australiensis*, has been recorded from West Dale (circle). Three fossil localities that have yielded macrofossils of *C. serratifolia* (squares) occur within Tasmania (inset) while all others occur on mainland Australia. Refer to text and figure 4.17 for the geological age of each fossil deposit.


Codia
c. 11 species
Stuart Creek
West Dale
Callicoma serratifolia
Berwick Quarry

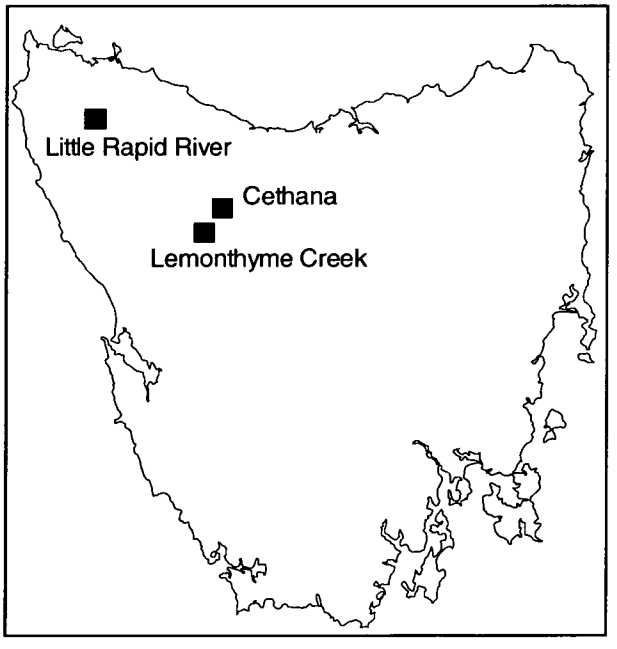
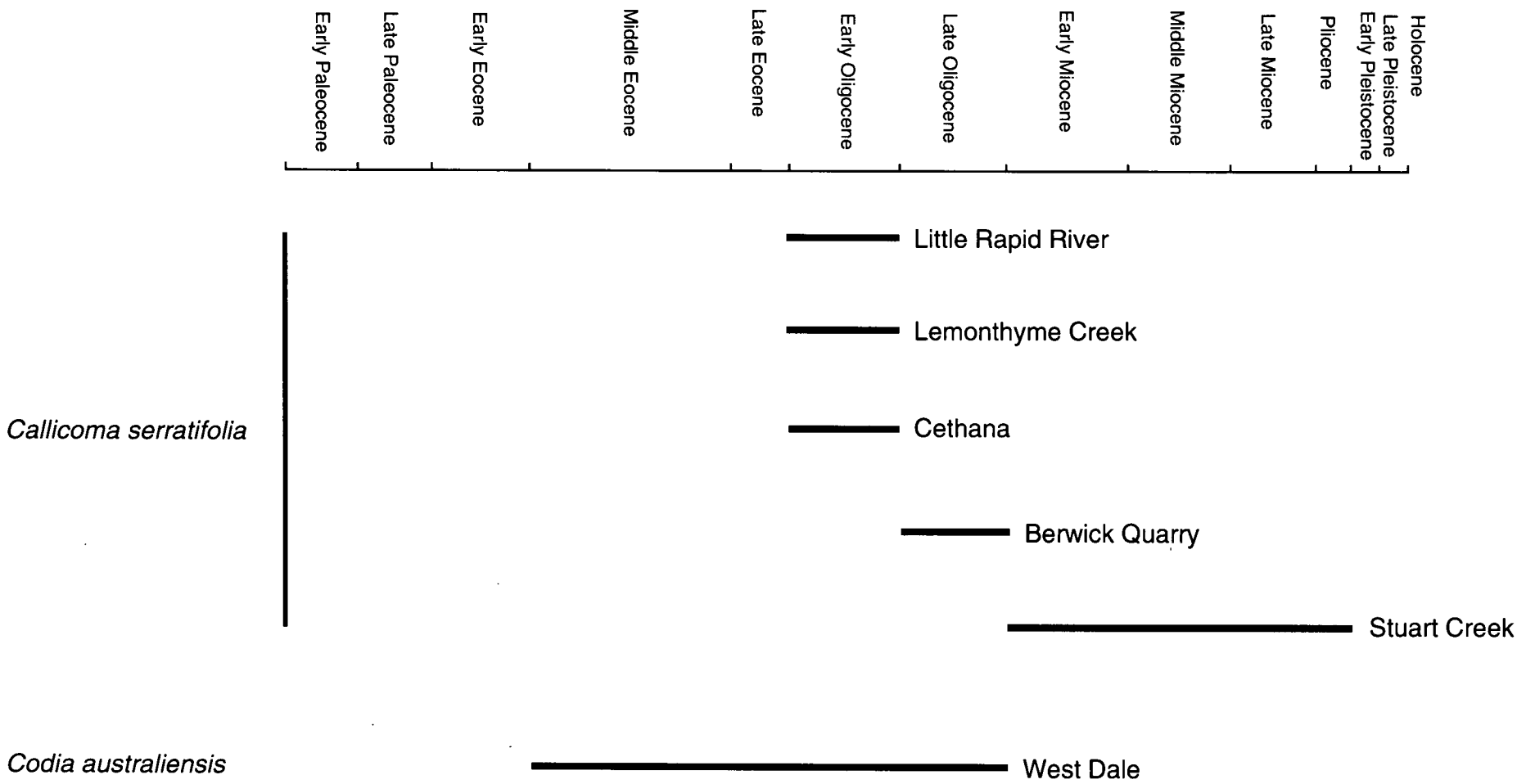

Little Rapid River
Cethana
Lemonthyme Creek

Fig. 4.17. Time sequence showing the stratigraphic age range of macrofossils of *Callicoma serratifolia* and *Codia australiensis.* The Little Rapid River and Cethana localities contain both leaf and infructescences macrofossils. Refer to figure 4.16 for the geographic location of fossil deposits.


Early Paleocene
Late Paleocene
Early Eocene
Middle Eocene
Late Eocene
Early Oligocene
Late Oligocene
Early Miocene
Middle Miocene
Late Miocene
Pliocene
Early Pleistocene
Late Pleistocene
Holocene
Little Rapid River
Lemonthyme Creek
Cethana
Berwick Quarry
Stuart Creek
Callicoma serratifolia
West Dale
Codia australiensis

If the macrofossils do represent the extant species then it had evolved prior to the Early Oligocene and has since remained relatively unchanged. *Callicoma serratifolia* was both temporally and spatially widespread during the Cainozoic and has since become restricted to eastern Australia (Figs 4.16 and 4.17). The climate of the Australian continent has changed significantly during this period (e.g. Truswell 1993; Quilty 1994) and has no doubt been one of the driving forces affecting plant distribution and dispersal capacity. The species in all fossiliferous deposits, except for Stuart Creek, occurred with other prominent Australian Cainozoic rainforest genera that have either experienced a similar decline in geographic distribution (e.g. *Agathis, Nothofagus* and *Gymnostoma*; see Scriven and Christophel 1990; Hill and Merrifield 1993, Pole *et al.* 1993) or complete extinction from Australia (e.g. *Dacrycarpus* and *Acmopyle*; see Hill and Carpenter 1991; Jordan 1995*b*; Hill and Whang 2000). The intra-generic evolution of leaf shape, form and size during the Cainozoic has been demonstrated in some of these genera, for example, *Nothofagus* (Hill 1983*a*, 1983*b*, 1994; Scriven and Hill 1996), *Acmopyle* and *Dacrycarpus* (Hill and Carpenter 1991), *Eucryphia* (Hill 1991*a*; Taylor and Hill 1996; Chapter 5 this study) and Casuarinaceae (Hill 1994), and has been hypothesised to be in response to a changing climate (e.g. Hill 1994 and authors cited therein). For *Callicoma serratifolia* there has been negligible morphological change over this time period, and the species may have migrated across the landscape to follow suitable climates rather than adapt to new ones.

Of particular significance is the recent (Miocene to Pliocene) occurrence of *C. serratifolia* in South Australia, which is clearly outside its modern geographic range (Fig. 4.16). The Stuart Creek macroflora is poorly studied but it is known to contain abundant leaves and fruits with strong affinities to extant *Eucalyptus*, leaves of *Brachychiton* (Sterculiaceae), *Cochlospermum* (Cochlospermaceae), *Banksieaeformis*, ?Lauraceae, Proteaceae (cf. *Orites*), and other unidentified broad-leaf angiosperm leaves and fruits (Greenwood *et al.* 1990; Greenwood 1996; Rowett 1997). This an is extremely different flora compared to that preserved in other deposits which contain *C. serratifolia* and has been suggested by Rowett (1997) to indicate the presence of marginal monsoonal forest with well-defined tropical and sclerophyllous elements, with most of the broad leaf plants growing along the watercourses. The occurrence of *C. serratifolia* in this forest type and hypothetical climatic envelope (Greenwood 1996) is in contrast to its current wet forest habitat of eastern Australia (e.g. Floyd 1989). Its relatively recent extinction from South Australia at least, may have been due to the continual drying of the Australian interior, in conjunction with increased seasonality. However, if the species did grow in such marginally dry and seasonal climates, as indicated by the Stuart Creek macroflora (Rowett 1997), then it can be argued that *C.*

serratifolia is not fully occupying its potential habitat and climatic range. The species may have become restricted or bottle-necked into its existing geographic location or habitat type and has since not expanded into all suitable sites, possibly due to its limited dispersal ability or from competition with other plants already existing in those niches.

4.5.4 Macrofossils of *Codia*

The single leaf macrofossil from West Dale assigned to the new species *Codia australiensis* has very close affinities to the juvenile foliage of at least one species of *Codia*. This represents the first fossil record of *Codia* and indicates an Early Cainozoic origin of the genus at the least. During the Cainozoic the genus had a different or more widespread or different distribution compared to its current geographic range (see Fig. 4.16) which may be further supported by a detailed study of the dispersed cuticle from the Oligocene-Early Miocene Morwell Formation that Blackburn (1985) described as aff. *Callicoma*.

Despite close affinities to juvenile *Codia* foliage, the fossil is unlikely to be a juvenile leaf as these would be an extremely rare component of any fossil deposit. This, combined with the absence of macrofossils comparable to adult *Codia* leaves in the West Dale deposit, suggests that the fossil may represent the adult foliage of an extinct *Codia* species, a possible ancestor or an extinct sister genus. The small size of the fossil (c. 50 mm long) cannot be used to either interpret the developmental age of the leaf or invoke a possible taphonomic bias towards small, possibly juvenile, leaves as these are often larger than adult foliage among the extant species. Also, other large, broad leaf specimens are preserved in the West Dale macroflora (e.g. *Myrtaciphyllum* and *Laurophyllum* species, Hill and Merrifield 1993).

Codia australiensis from West Dale indicates that the genus or, at the least, a sister genus did not evolve in isolation in New Caledonia where it is now endemic (Rao and Dickison 1985*b*). This fossil is therefore of palaeobiogeographical significance as it demonstrates that the extant genus or ancestor to both genera was either (i) present on both land masses (Australia and New Caledonia) prior to the breakup of Gondwanaland (i.e. vicariance), or was (ii) present on one land mass and dispersed to the other, having later become extinct from Australia (i.e. dispersal). For vicariance, the ancestor or extant genus has to be at least 70-90 million years old as this is approximately when Australia and Antarctica became isolated from both New Zealand and New Caledonia (see Stevens 1989). The age of the West Dale deposit (Middle

Eocene-Late Oligocene) does not support or refute this hypothesis although older *Codia* macrofossils may exist but have not been located. It is possible that *Codia* evolved within Australia or New Caledonia and dispersed to the other land mass. *Codia* has been described by Dickison (1984) to have wind dispersed indehiscent fruits as they possess a dense covering of woolly hairs, although they may equally be dispersed by water. The importance of long distance dispersal in the colonisation ability of *Weinmannia* throughout the South Pacific Islands has been discussed by Bradford (1998) and Hopkins (1998*a*), and its importance in other Cunoniaceae genera in the past cannot be underestimated (see Chapter 7).

4.5.5 Evolutionary Significance of *Callicoma* and *Codia* Macrofossils

A stomatal cutin frill/ledge and paired trichomes were recorded in *Callicoma serratifolia* and some *Codia* species by Carpenter and Buchanan (1993) who suggest that there is doubt that such distinct cuticle morphology arose independently in *Codia* and *Callicoma*. The leaf morphological results presented here support the hypothesis of Carpenter and Buchanan (1993) that the independent evolution of these two structures in separate lineages is unlikely, and therefore suggest a close phylogenetic relationship of the genera, but convergent evolution cannot be totally excluded.

A hypothesis for the evolution of these genera, based on cuticular characters and the West Dale fossil, is that the ancestor to both genera had a stoma cutin ledge/frill and paired trichome bases, which have been secondarily lost within some *Codia* species. This hypothesis has been supported by recent analyses combining molecular and morphological datasets, to which this study has contributed (see Bradford and Barnes manuscript submitted, Appendix 1). All three genera occur in the tribe Codieae G.Don, with *Pullea* basal to the sister taxa *Codia* and *Callicoma*. The phylogeny indicates that a stoma cutin frill/ledge evolved once in the ancestor to both *Callicoma* and *Codia* (see Fig. 4.18). Although these two structures are plesiomorphies for these genera, it can be stated that the loss of these structures has occurred in most *Codia* species but it is unknown if secondary loss has occurred more than once within *Codia*.

The ancestor to both genera was probably dimorphic for leaf from (Fig. 4.18). This dimorphism in the ancestor may have been expressed as heteroblasty, where there is a distinct juvenile and adult leaf form. This has subsequently been lost within *C. serratifolia* which is now considered to be homoblastic, and may indicate that the species had a paedomorphic origin from the ancestor to both genera, although other heterochronic processes may have been involved. *Callicoma serratifolia* may have

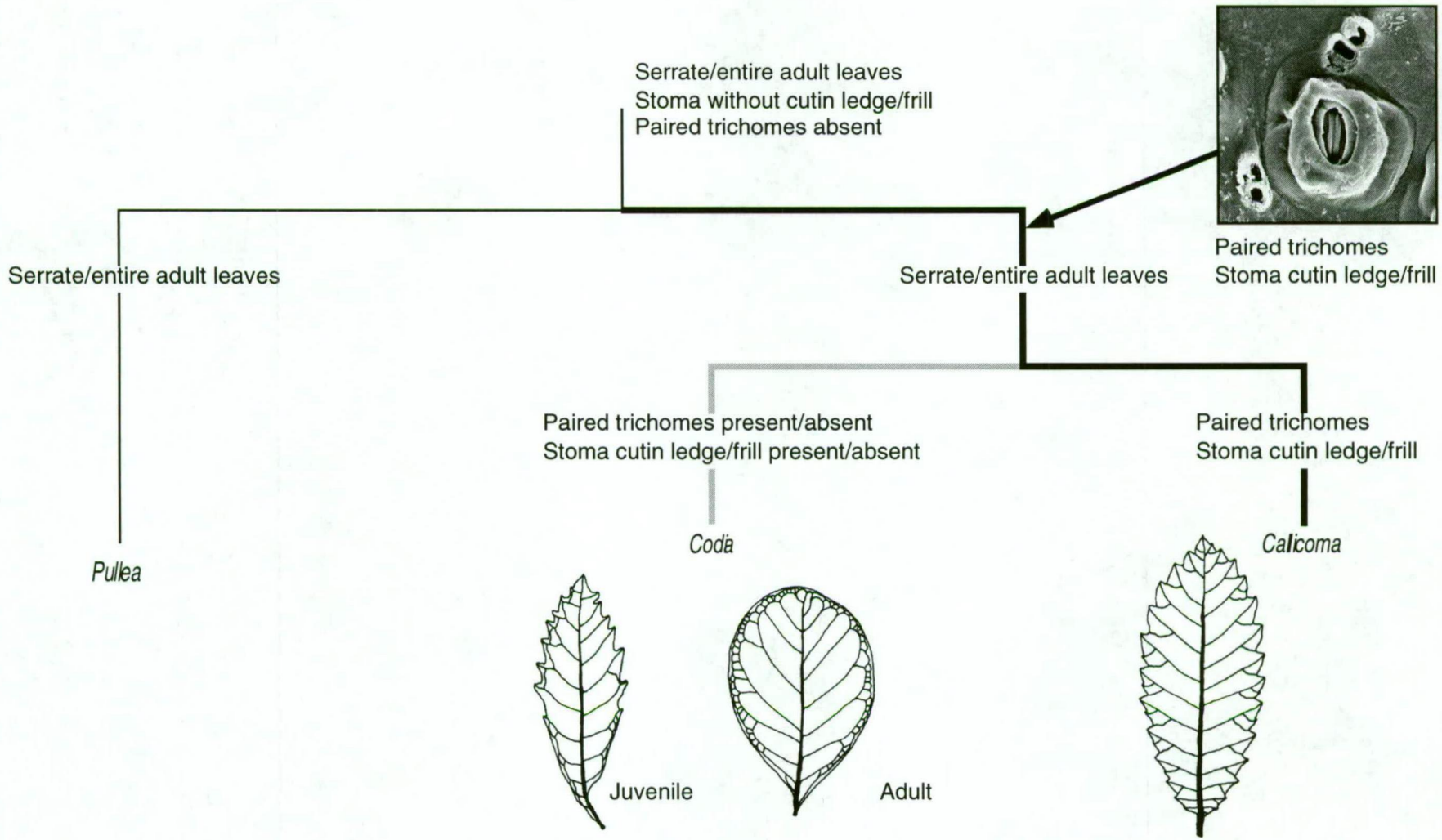
Fig. 4.18. A cladogram of the genera within the tribe Codieae. This cladogram is a subsection of the strict consensus tree produced from a parsimony analysis of morphological characters at the generic level for all Cunoniaceae genera using a constraint tree based on clades supported by molecular data (see Bradford and Barnes manuscript submitted, Appendix 1).

The line drawings of leaves next to each genus represent the leaf form in that particular genus for each life stage, if present. The inset figure illustrates the cutin ledge and small paired trichome bases in *Codia discolor*.

The cladogram indicates that the ancestor to the tribe Codieae was dimorphic for adult leaf form, it had stoma without a cutin frill/ledge and paired hair bases were absent. These plesiomorphies are present in the basal taxon *Pullea*.

The ancestor to both *Codia* and *Callicoma* may have been heteroblastic, where there are distinct juvenile and adult leaves. Adult leaves of *Codia* have an entire margin while the juvenile leaves of at least one species are serrate. *Callicoma* with its homoblastic serrate leaves may have evolved by the retention of the juvenile foliage phase (paedomorphogenesis) from a common ancestor with *Codia*.

Based on the cladogram, a stoma cutin ledge/frill and small paired trichome bases evolved once in a common ancestor to both *Codia* and *Callicoma*. Within *Codia* there has been a reversion to stoma without a cutin ledge/frill and a loss of the small paired trichomes.


Serrate/entire adult leaves
Stoma without cutin ledge/frill
Paired trichomes absent
Paired trichomes
Stoma cutin ledge/frill
Serrate/entire adult leaves
Serrate/entire adult leaves
Paired trichomes present/absent
Stoma cutin ledge/frill present/absent
Paired trichomes
Stoma cutin ledge/frill
Pullea
Codia
Callicoma
Juvenile
Adult

evolved by the retention of the juvenile phase in a common ancestor with *Codia.* Indeed, the stoma cutin ledge/frill and paired trichome bases may be juvenile characters that are still expressed into the adult foliage of some *Codia* species although this is difficult to prove.

Although it is apparent that *Codia* did not evolve in isolation within New Caledonia it is likely that further evolution of leaf form and several aspects of leaf and/or floral morphology of the genus may have been in response to the unusual chemistry posed by the ultramafic soils of New Caledonia (Specht 1979; Baker and Brooks 1988). This is perhaps supported by a more advanced wood (Ingle and Dadswell 1956; Dickison 1980*b*) and floral (Dickison 1984) morphology than *Callicoma serratifolia* (see Bradford and Barnes manuscript submitted, Appendix 1).

Chapter 5. Leaf and Reproductive Macrofossils of *Eucryphia*

5.1 Introduction

Eucryphia is biogeographically discontinuous with five species in Australia (Fig. 5.1) and two in South America. On mainland Australia, *Eucryphia moorei* is a canopy tree of warm and cool temperate rainforest of southern New South Wales and Victoria (Harden 1990*c*; Fig. 5.1). The two rare species, *E. jinksii* and *E. wilkiei*, are represented by single populations. *Eucryphia jinksii* occurs as a large tree in complex notophyll vine forest at an altitude of 770-800 m a.s.l. in the McPherson Ranges while *E. wilkiei* occurs as a small multi-stemmed tree on the eastern slope of Mt. Bartle Frere in north-eastern Queensland between 1200 and 1400 m a.s.l. in microphyll vine thicket (Forster and Hyland 1997).

In Tasmania, *Eucryphia lucida* occurs as a canopy tree within lowland cool temperate rainforest of western and southern Tasmania (Boland *et al.* 1985; Read and Busby 1990), only rarely occurring in the subalpine climatic zone (>900 m a.s.l.). *Eucryphia milliganii* is endemic to Tasmania and has recently been separated into two distinct subspecies by Barnes *et al.* (2000) based on leaf shape and pubescence. *Eucryphia milliganii* ssp. *milliganii* has oblong, almost glabrous leaves and occurs in western Tasmania while *E. milliganii* ssp. *pubescens* has ovate-elliptic leaves with pubescent margins and abaxial lamina and occurs in southern and south-western Tasmania. Both subspecies predominantly occur at higher altitudes (>700 m a.s.l.) or on exposed or poorly drained sites. In lowland riparian localities both subspecies rarely grow together (see Barnes *et al.* 2000) but do frequently occur with *E. lucida.*

In South America, *Eucryphia cordifolia* occurs as a canopy tree in the wet cool temperate Valdivian forests to the west of the Andes between 35° 30' and 42° S and in the north-western corner of Chilóe Island (Holdgate 1961; Veblen and Schlegel 1982; Rancusi *et al.* 1987; Zegers 1995). *Eucryphia glutinosa* is a comparatively rare shrub that grows between 250 and 900 m a.s.l. in the foothills of the Chilean Andes (approximately 36° to 39° S) and is winter semi-deciduous (Rodriguez *et al.* 1983; Rancusi *et al.* 1987; Zegers and Garcia 1994), a feature unique to this species within the Cunoniaceae.

Florally, *Eucryphia* is characterised by axillary solitary flowers that have 4 to 5 enlarged and showy white petals (Fig. 5.2.a-c). The flowers are ploystemonous with

Fig. 5.1. Past and present distribution of *Eucryphia* in eastern mainland Australia and Tasmania (inset). Fossil localities of the genus are shown as squares. The distribution of widespread species are shaded, those of restricted species are shown as circles. The subspecies of *E. milliganii* differ in their distribution in Tasmania; *E. milliganii* ssp. *milliganii* occurs in the north-west and west while *E. milliganii* ssp. *pubescens* occurs in the south and south-west. *Eucryphia lucida* occurs throughout the range of both *E. milliganii* subspecies. The Regatta Point locality represents Early Eocene sediments overlain with glacial outwash containing clasts of Early Pleistocene and Early-Middle Pleistocene age. Geological ages for localities are listed in Table 5.1.

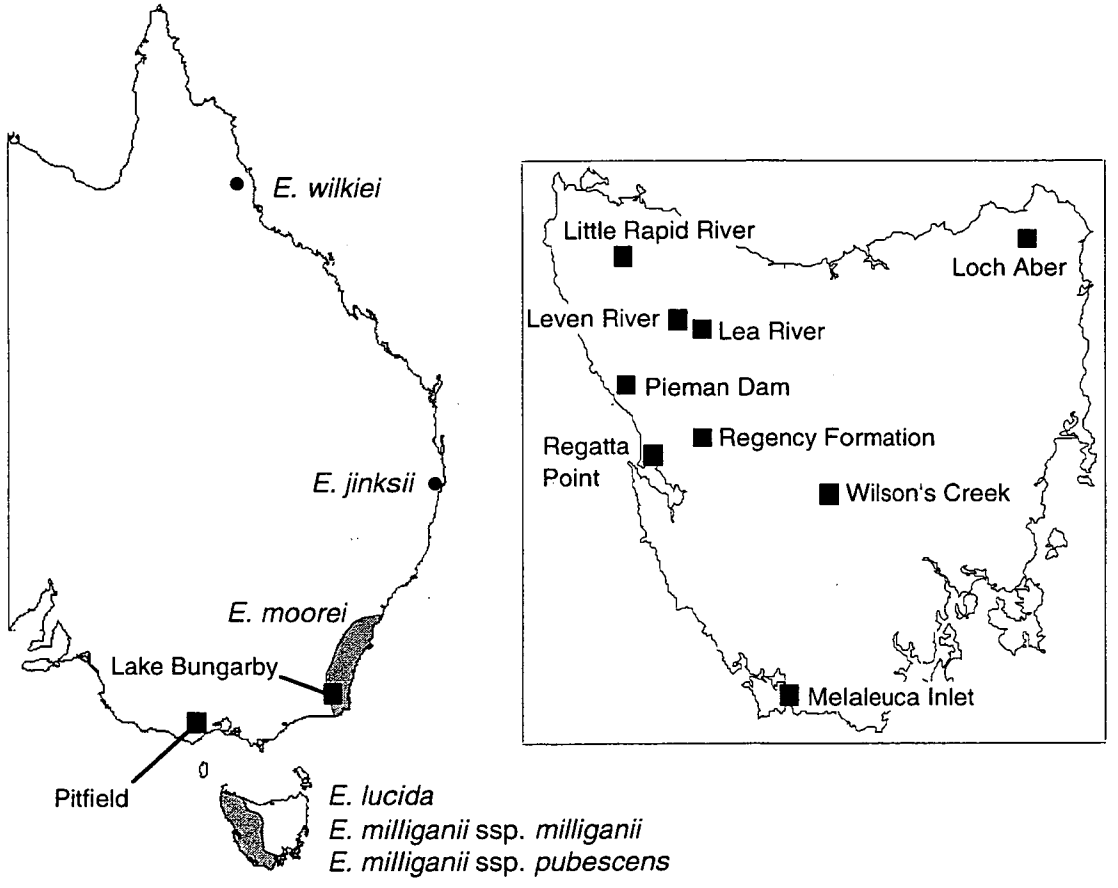

E. wilkiei
E. jinksii
E. moorei
Lake Bungarby
Pitfield
E. lucida
E. milliganii ssp. milliganii
E. milliganii ssp. pubescens
Little Rapid River
Loch Aber
Leven River
Lea River
Pieman Dam
Regency Formation
Regatta Point
Wilson's Creek
Melaleuca Inlet

Fig 5.2 a-f. Flowers and capsules of selected extant *Eucryphia* species. Scale bar for all = 10 mm.

Fig. 5.2.a. *Eucryphia wilkiei* from north-eastern Australia. Note the bright yellow nectar at the base of the anthers and central polycarpelous ovary.

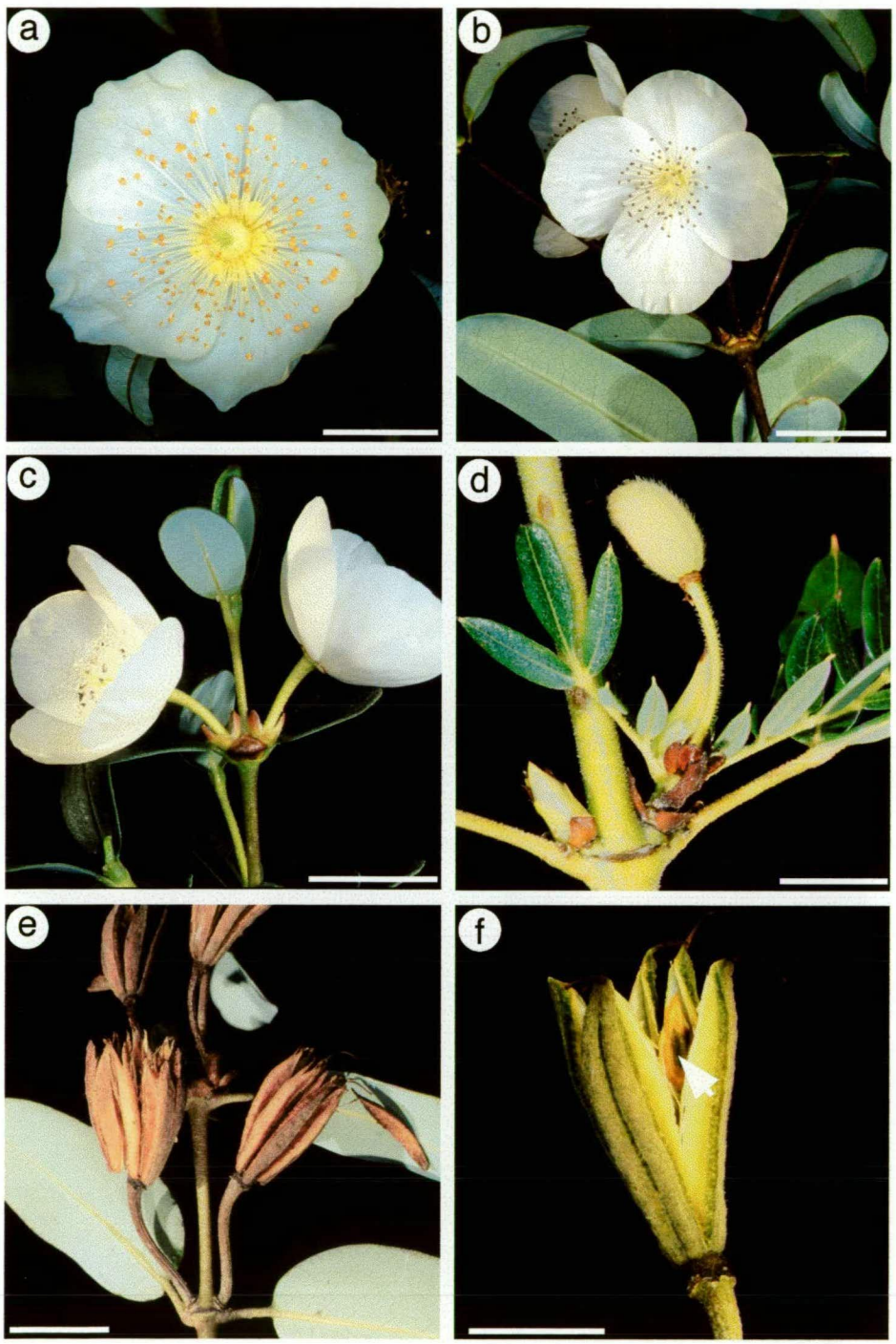
Fig. 5.2.b. *Eucryphia lucida* from Tasmania.

Fig. 5.2.c. *Eucryphia milliganii* ssp. *milliganii* from Tasmania. Note the solitary flowers and the presence of paired floral bracts at the base of the pedicel.

Fig. 5.2.d. An immature capsule in *E. moorei* from south-eastern Australia.

Fig. 5.2.e. Mature capsules in *E. lucida*. As capsules become older they tend to fall apart, shedding the boat-shaped valves (far right). Seeds have generally fallen out prior to the shedding of valves.

Fig. 5.2.f. A dehisced capsule of *E. lucida*. Note the septicidal dehiscence and the presence of a small winged seed (arrow) in a single valve. The endocarp and exocarp are fused but remain distinct at fruit maturity.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a superior ovary that is composed of multiple fused carpels (Fig. 5.2.b), ranging from 4 to 12 depending on the species (Bausch 1938; Taylor 1993), but may be as high as 18 (Bausch 1938). The flowers are borne on pedicels that have basal bracts (Fig. 5.2.c). The fruit is a variably pubescent woody capsule that dehisces septicidally at maturity (Figs 5.2.d-f). As the capsule ages it sheds the boat shaped valves (Fig. 5.2.e), usually before all the winged seeds (Fig. 5.2.f) have been released.

All species are evergreen except for *E. glutinosa* which is semi-winter deciduous (Zegers and Garcia 1994). Leaves in all species are opposite and decussate in arrangement, with prominent interpetiolar stipules that can be large and leafy (Fig. 5.3.b-c) or small and caducous (Fig. 5.3.d). Leaves are compound or simple, with either serrate or entire margins (Fig. 5.3.e-i). The adult leaves of *E. cordifolia* (Fig. 5.3.e) and *E. glutinosa* (Fig. 5.3.f) are irregularly serrate, while those of all Australian species are entire, although the juvenile leaves of at least *E. moorei, E. lucida* and the subspecies of *E. milliganii* have toothed apices (Hill 1991*a*; R. W. Barnes pers. obs.).

Eucryphia has a very extensive fossil record with macrofossils identified from 11 Cainozoic deposits in south-eastern Australia (Tables 5.1 and 5.2). All described macrofossil species prior to this study, except for *E. gregorii*, are represented by leaves or leaf fragments with cuticle preserved and possess simple unicellular trichome bases, stoma with a brachyparacytic subsidiary cell arrangement, and abaxial peltiform cuticular extensions to some extent (Hill 1991*a*), which form the basis of most identifications. Hill (1991*a*) provides a detailed morphological account of extant *Eucryphia* leaves and how to identify evergreen leaf macrofossils of the genus (Table 5.3). The most distinctive feature of extant evergreen *Eucryphia* species is the presence of abaxial peltiform extensions (Fig. 5.4.a-b), which are described by Hill (1991*a*) as outgrowths of the epidermal cell. These extensions are absent from the winter deciduous species *E. glutinosa* (Fig. 5.4.c) which may represent a reversion to the ancestral form based on the cladogram of Taylor and Hill (1996) although, they may equally be absent due to the species' semi-deciduous habit. The subsidiary cell arrangement in *Eucryphia* is brachyparacytic (Fig. 5.4.d), and hair bases are always unicellular (Figs 5.4.a-b, e-f) and are most common on the abaxial veins (Fig. 5.4.a), midrib and leaf margin. The adaxial epidermal cells are typically isodiametric in shape and hair bases are present, but are variable in density among the extant species (Fig. 5.4.f).

The oldest fossil *Eucryphia* species, *E. falcata* from Lake Bungarby (Late Paleocene), has compound leaves consisting of possibly five leaflets. It probably resembles the ancestral leaf form of the genus, which is serrate and falcate (see Taylor and Hill

Fig 5.3 a-d. Stipule shape and form in selected extant *Eucryphia* species.

Fig. 5.3.a. Interpetiolar stipules occur between the opposite decuassately arranged compound leaves in *E. jinksii* from eastern Australia. Scale bar = 30 mm.
Fig. 5.3.b. Closeup of the large interpetiolar stipules in *E. jinksii*. Stipules are thin and have pubescent margins. The stems and leaves are also highly pubescent. Scale bar = 10 mm.
Fig. 5.3.c. Small interpetiolar stipule (arrow) in *E. wilkiei* from Mt Bartle Frere in north-eastern Australia. The compound leaves are highly tomentose when they emerge from the new bud. Scale bar = 20 mm.
Fig. 5.3.d. Small interpetiolar stipule (arrow) in *E. milliganii* ssp. *milliganii* from Tasmania. Stipules are shortly triangular in shape and generally become brown prior to shedding. Scale bar = 5 mm.

Figs 5.3.e-i. Cleared leaves and leaflets of extant *Eucryphia* species showing venation patterns and margin form.

Fig. 5.3.e. Simple leaf of *E. cordifolia* from Chile, South America. Note the irregularly serrate margin and lobate leaf base. Secondary venation is semicraspedodromous. Scale bar = 30 mm.
Fig. 5.3.f. Terminal leaflet of the winter deciduous species *E. glutinosa* from Chile, South America. Leaflets have coarsely serrate margins and craspedodromous venation. Scale bar = 10 mm.
Fig. 5.3.g. Terminal leaflet of *E. jinksii* from eastern Australia. The leaf margin is entire and secondary venation is brochidodromous. Scale bar = 10 mm.
Fig. 5.3.h. Simple leaf of *E. lucida* from Tasmania. Secondary venation is predominantly reticulodromous. Scale bar = 10 mm.
Fig. 5.3.i. Simple leaf of *E. milliganii* ssp. *pubescens* from Tasmania. Note the ovate leaf shape and prominent emarginate leaf apex. Secondary venation is reticulodromous. Scale bar = 10 mm.

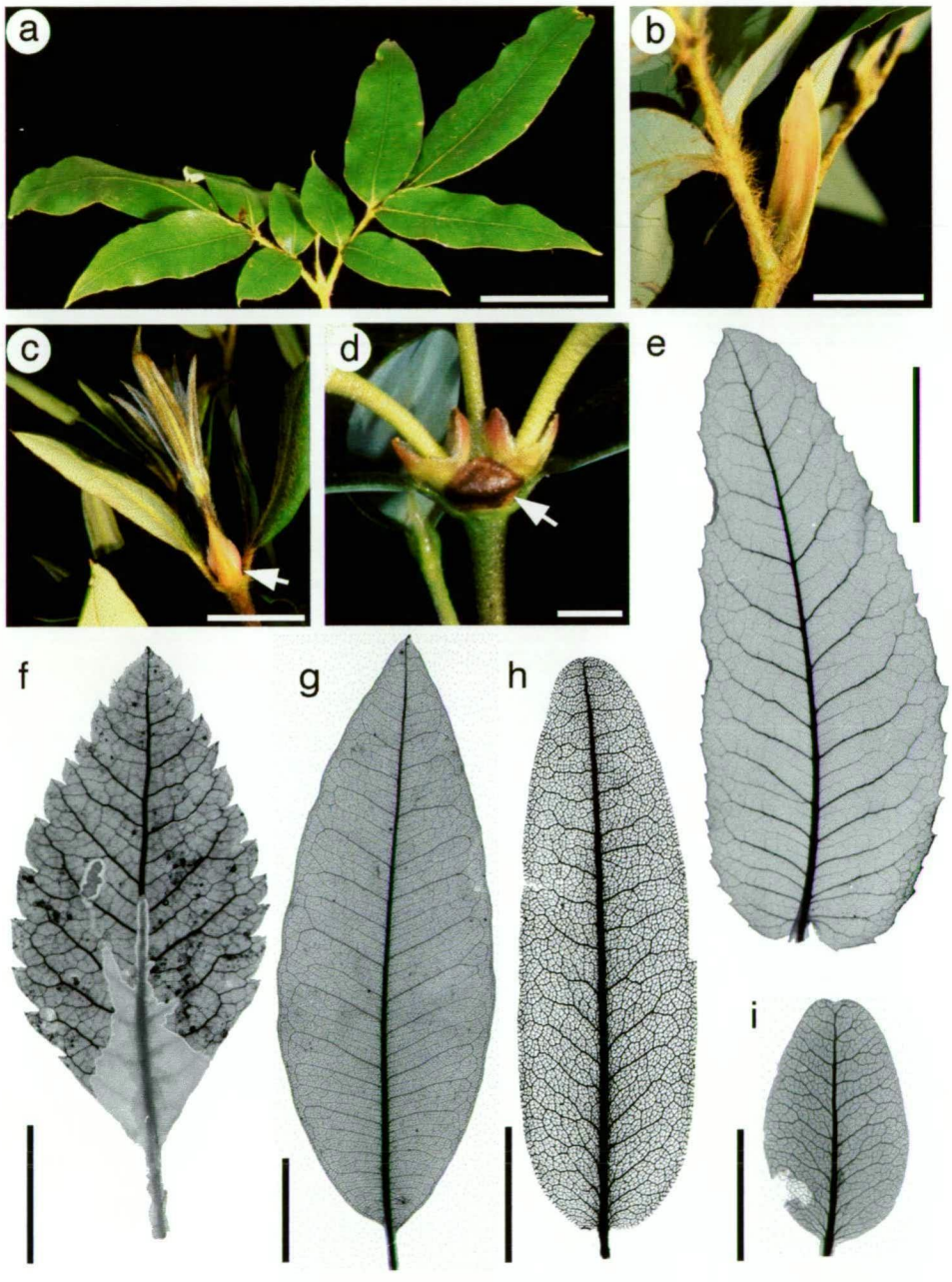
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Table 5.1. Geological age for deposits that contain *Eucryphia* macrofossils

Three separate fossiliferous deposits occur at Regatta Point, western Tasmania. Refer to Table 5.2 for key references to deposit ages and the previously described *Eucryphia* macrofossils that each contain.

Deposit location	Geological age
Lake Bungarby, New South Wales	Late Paleocene
Pitfield, Victoria	Tertiary
Regatta Point, western Tasmania	Early Eocene, Early Pleistocene and Early-Middle Pleistocene
Loch Aber, north-eastern Tasmania	Middle to Late Eocene
Little Rapid River, north-western Tasmania	Early Oligocene
Wilson's Creek, central Tasmania	?Latest Eocene-Early Oligocene
Lea River, north-western Tasmania	Early Oligocene
Leven River, north-western Tasmania	Early Oligocene
Regency Formation, western Tasmania	Middle Pleistocene
Melaleuca Inlet, south-western Tasmania	Late Pleistocene
Pieman Dam, western Tasmania	Late Pleistocene

Table 5.2. Macrofossil records of *Eucryphia* from south-eastern Australia

Three separate fossiliferous deposits occur at Regatta Point; Early Eocene [A] sediments overlain by glacial outwash that contains clay clasts of Early Pleistocene [G] and Early-Middle Pleistocene [E] age.

Source: [A] Hill 1991*a*; [B] Deane 1902*c*; [C] Carpenter and Jordan 1997; [D] Taylor 1993; [E] Jordan *et al.* 1995; [F] Fitzsimons *et al.* 1990; [G] Jordan 1992; [H] Jordan *et al.* 1991; [I] Colhoun 1980.

Taxon	Macrofossil type	Geological age	Fossil locality
Eucryphia falcata [A]	Leaf compressions	Late Paleocene	Lake Bungarby, New South Wales
E. gregorii [B]	Leaf impression	Tertiary	Pitfield, Victoria
E. microstoma [A]	Leaf compression	Early Eocene	Regatta Point, western Tasmania
E. aberensis [A]	Mummified leaf fragments	Middle to Late Eocene	Loch Aber, north-eastern Tasmania
E. sp. [C]	Dispersed cuticle	Early Oligocene	Leven River, north-western Tasmania
E. aff. *milliganii* [AD]	Mummified leaves	Early Pleistocene	Regatta Point, western Tasmania
E. sp. [E]	Dispersed cuticle	Middle Pleistocene	Regatta Point, western Tasmania
E. lucida [DFG]	Mummified leaves	Middle Pleistocene	Regency, western Tasmania
E. milliganii [DFG]	Mummified leaves	Middle Pleistocene	Regency, western Tasmania
E. sp. [H]	Dispersed cuticle	Late Pleistocene	Melaleuca Inlet, south-western Tasmania
E. lucida [I]	Mummified leaves	Late Pleistocene	Pieman Dam, north-western Tasmania

Table 5.3. Morphological features typical of extant evergreen *Eucryphia* leaves that are useful in identifying leaf macrofossils
Characters in bold form the basis of all currently accepted identifications of *Eucryphia* leaf macrofossils. Data obtained from Hill (1991*a*) and this study.

Feature/structure	Description
Leaves	Compound or simple; leaf margin serrate or entire.
Secondary venation	Brochidodromous, semicraspedodromous or reticulodromous.
Stomata	**Brachyparacytic subsidiary cell arrangement.**
Abaxial surface	**Peltiform cuticular extensions on epidermal cells, and occasionally on venal cells.**
Hair bases	Simple, no basal foot cell, 5-7 radially modified epidermal cells.

Figs 5.4.a-f. Cuticle features of several extant *Eucryphia* species.

Fig. 5.4.a. Outer abaxial cuticle of *E. moorei* showing well developed cuticular peltiform extensions. Note large unicellular hair bases on veins (arrow). Scale bar = 250 μm.

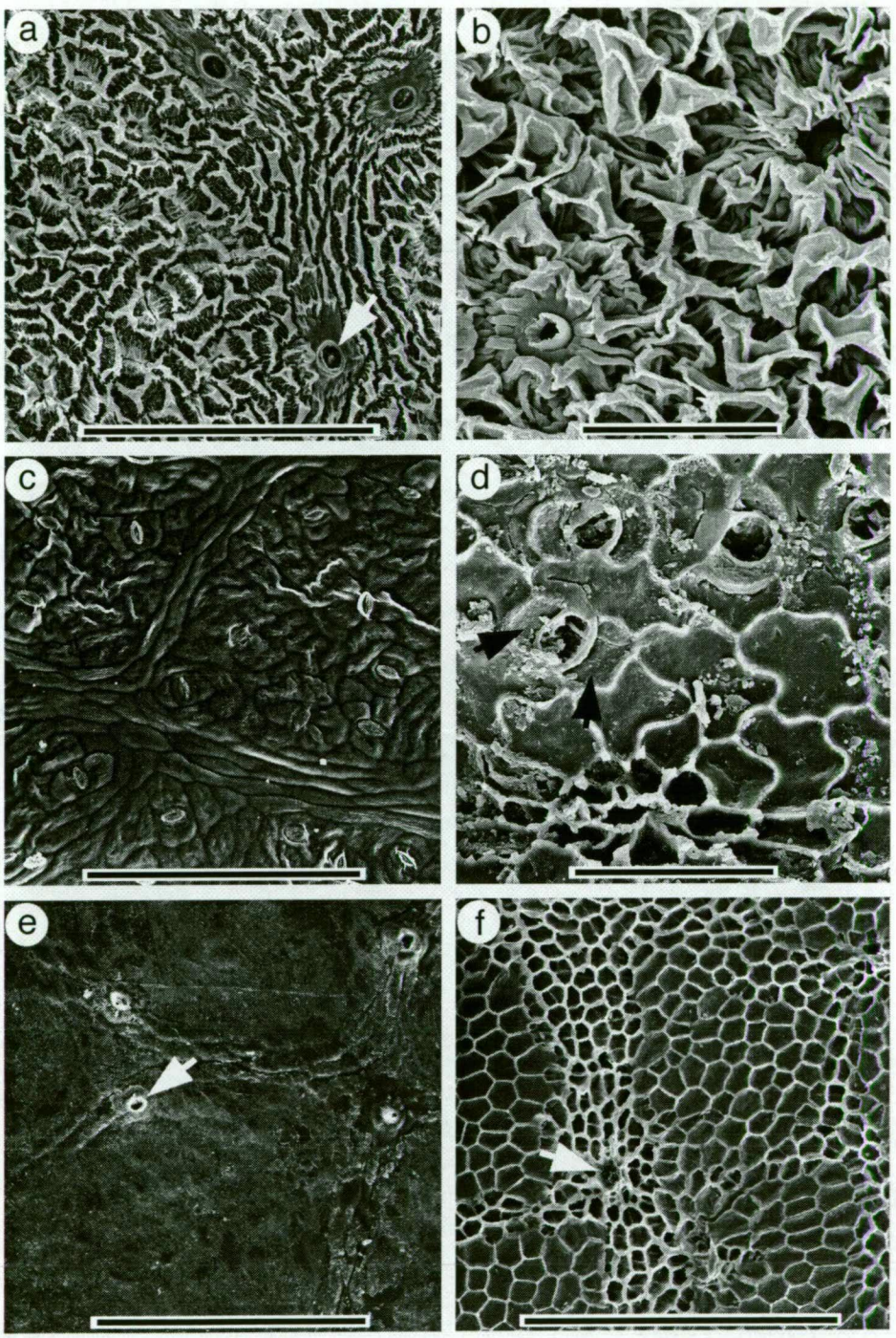
Fig. 5.4.b. Outer abaxial cuticle of *E. jinksii* showing a unicellular hair base (lower left) and hydathode (top right). The cuticular peltiform extensions are well developed and obscure the stomata, as can be seen around the hydathode. Scale bar = 50 μm.

Fig. 5.4.c. Outer abaxial cuticle of *E. glutinosa*. The epidermal cells are slightly raised but do not possess the distinctive cuticular peltiform extensions that occur in the evergreen species. Scale bar = 150 μm.

Fig. 5.4.d. Inner abaxial cuticle of *E. jinksii*. Note the unicellular hair base (lower left) and stomata with a brachyparacytic subsidiary cell arrangement (arrows indicate the position of the subsidiary cells). Scale bar = 50 μm.

Fig. 5.4.e. Outer adaxial cuticle of *E. moorei* showing unicellular hair bases on the veins (arrow). Scale bar = 150 μm.

Fig. 5.4.f. Inner adaxial cuticle of *E. cordifolia* showing isodiametric epidermal cells between veins composed of smaller epidermal cells. The inner surface of a unicellular hair base is indicated by the arrow. Scale bar = 250 μm.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1996). The Early Eocene Regatta Point species *E. microstoma* has unusually small stomata (Hill 1991*a*) and may not even represent *Eucryphia*.

Macrofossils of *Eucryphia* from Early Pleistocene Regatta Point sediments have been extensively studied (Hill and Macphail 1985, Hill 1991*a*, Jordan 1992, Taylor 1993). Hill (1991*a*) assigned the fossils to *E.* aff. *milliganii* as they may equally represent leaves of *E. milliganii* or a form that immediately preceded that observed in *E. lucida*. Macrofossils conspecific to the two extant Tasmanian species *E. lucida* and *E. milliganii* have been located in the Middle Pleistocene Regency Formation (Fitzsimons *et al.* 1990; Jordan 1992; Taylor 1993) and those of *E. lucida* have been recovered from Late Pleistocene sediments at the Pieman Dam (Colhoun 1980), both in western Tasmania (see Fig. 5.1). *Eucryphia gregorii* was described by Deane (1902*c*) from Cainozoic sediments at Pitfield in southern Victoria.

This study describes three new macrofossil species of *Eucryphia* from Tasmanian Cainozoic localities, including the first fossil capsules ever recorded. The macrofossils described by Hill (1991*a*) as *Eucryphia* are also re-examined, with particular emphasis on *E. aberensis* from Loch Aber and *E.* aff. *milliganii* from the Early Pleistocene sediments at Regatta Point.

5.2 Materials and Methods

5.2.1 Extant Specimens

Fresh and dried herbarium specimens of all extant species were available for this study. Leaves of *E. lucida, E. moorei, E. glutinosa, E. cordifolia* and the two subspecies of *E. milliganii, E. milliganii* ssp. *milliganii* and *E. milliganii* ssp. *pubescens* (see Barnes *et al.* 2000), were examined from the herbarium and living collection housed at the School of Plant Science, University of Tasmania. Leaves of *E. wilkiei* were collected from the only known population (17°24'30" S, 145°49' E; Fig. 5.1). Leaves of *E. jinksii* were collected from Natural Arch National Park, Springbrook (28°14' S, 153°13' E; Fig. 5.1) by P. I. Forster and preserved in 5:5:90 40% formalin-acetic acid-alcohol solution (FAA). Specimens examined covered the geographic range of each species.

5.2.2 Fossil Localities and Specimens

All *Eucryphia* fossil localities, with the exception of Lake Bungarby and Pitfield, occur within Tasmania (Fig. 5.1; Tables 5.1 and 5.2). All macrofossils were photographed with a Canon EOS camera using a low angle light source. The cuticle of fossil and extant specimens is outlined in '2.2.1 Cuticle Preparation'.

5.2.2.1 Lea River, north-western Tasmania

A fossil capsule (Lea-3301) and a leaf fragment (Lea-3302) assignable to *Eucryphia* were extracted from macerated sediment and are Early Oligocene in age.

5.2.2.2 Wilson's Creek, central Tasmania

A single compression fossil of a *Eucryphia* leaf (WC-33) was extracted and is ?Latest Eocene-Early Oligocene in age.

5.2.2.3 Loch Aber, north-eastern Tasmania

The locality is Middle to Late Eocene in age (see Hill and Christophel 1988). The specimens of *E. aberensis* that were examined by Hill (1991*a*) were available for this study in addition to specimens from more recent collections of the locality. An emended diagnosis for *E. aberensis* is presented.

5.2.2.4 Little Rapid River, north-western Tasmania

Several leaf fragments and a capsule which are assignable to *Eucryphia* were examined from this Early Oligocene deposit.

5.2.2.5 Regatta Point, western Tasmania

Three fossiliferous deposits occur at Regatta Point. *Eucryphia microstoma* (Hill 1991*a*) has been described from the abundant Early Eocene sediments at this site. Glacial outwash that overlays these sediments contains clay clasts of Early Pleistocene and Early-Middle Pleistocene age (see Tables 5.1 and 5.2). Dispersed cuticle of *Eucryphia* has been recorded from the Early-Middle Pleistocene clasts (Jordan *et al.*

1995). The Early Pleistocene clasts are primarily aged on palynostratigraphy (Macphail *et al.* 1993*b*; Jordan and Hill 1994) and contain mummified leaves and leaf fragments of *Eucryphia* that have been studied by Hill and Macphail (1985), Hill (1991*a*), Jordan (1992), Taylor (1993) and Taylor and Hill (1996). Specimens from this deposit have the prefix RPE (Early Eocene), RPA (Early-Middle Pleistocene), or RPU (Early Pleistocene). All specimens were available for this study.

5.2.2.6 Regency Formation, western Tasmania

Leaf macrofossils of *Eucryphia* have been extracted from this Middle Pleistocene (Jordan and Hill 1994) deposit and studied by Fitzsimons *et al.* (1990), Jordan (1992) and Taylor (1993).

5.2.2.7 Leven River, north-western Tasmania

This Early Oligocene deposit (Carpenter and Jordan 1997; Jordan *et al.* 1998) contains dispersed cuticle (Lev-100, slides) that is assignable to *Eucryphia* and was examined during this study.

5.2.2.8 Pitfield, Victoria

Deane (1902*c*) described several fossil species from the Tertiary deposit, including a single incomplete leaf as *Eucryphia gregorii.*. The description and illustration by Deane (1902*c*) were used in this study as the original specimen could not be located.

5.3 Results

5.3.1 Lea River, north-western Tasmania

The fossil capsule shares many features with those of extant *Eucryphia* species, including the large number and shape of the valves, their dehiscence and attached apical style. Extant *Eucryphia* capsules are composed of 5-14 (-18) boat-shaped valves each with a terminal style (Bausch 1938; Dickison 1978; Harden 1990*c*; Figs 5.2.e-f and 5.5.a) that dehisce septicidally (Harden 1990*c*), with a vascular connective fused to the inner endocarp for the length of the valve (Fig. 5.5.b). This connective splits near the valve suture and continues to the apical style, along the inner edge of the

Figs 5.5.a-d. Capsule features of extant *Eucryphia lucida.*

Fig. 5.5.a. Whole capsule.
Fig. 5.5.b. Partially dissected capsule showing the thin vascular connective fused to the inner endocarp. Note the splitting of the connective near the valve suture (arrow). Scale bar for both = 10 mm.
Fig. 5.5.c. Scanning electron micrograph of the receptacle showing the pedicel (Pd), a prominent scar from a detached sepal (S) and petal insertion point (P). Scale bar = 500 μm.
Fig. 5.5.d. Unicellular hair base on exocarp. Scale bar = 25 μm.

Fig. 5.5.e. Dehisced capsule of *Geissois biagiana* showing terminal styles that split at fruit maturity (black arrow) and central vascular connective between the dehisced carpels (white arrow). Scale bar = 10 mm.

Figs 5.5.f-k. Holotype of *Eucryphia reticulata* R.W.Barnes & G.J.Jord. (Lea-3301) from Lea River, north-western Tasmania.
Fig. 5.5.f. Macrofossil with remnants of terminal style (arrow). Scale bar = 10 mm.
Figs 5.5.g-k. Scanning electron micrographs.
Fig. 5.5.g. Receptacle showing two prominent sepal scars (S) and adjacent petal insertion point. Scale bar = 500 μm.
Fig. 5.5.h. Side view of valve showing glabrous endocarp (En) and distinct exocarp (Ex). Scale bar = 200 μm.
Fig. 5.5.i. Unicellular hair base on exocarp. Scale bar = 25 μm.
Fig. 5.5.j. Side view of valve showing vascular connective (Vc) fused to the inner endocarp and connective bifurcation (B) near the valve suture (top right). Scale bar = 400 μm.
Fig. 5.5.k. Seed coats dissected from within the valves. Scale bar = 200 μm.

Figs 5.5.l, m. Scanning electron micrographs of the seed coat of selected extant *Eucryphia* species.
Fig. 5.5.l. *E. lucida.* Scale bar = 50 μm.
Fig. 5.5.m. *E. cordifolia.* Scale bar = 200 μm.

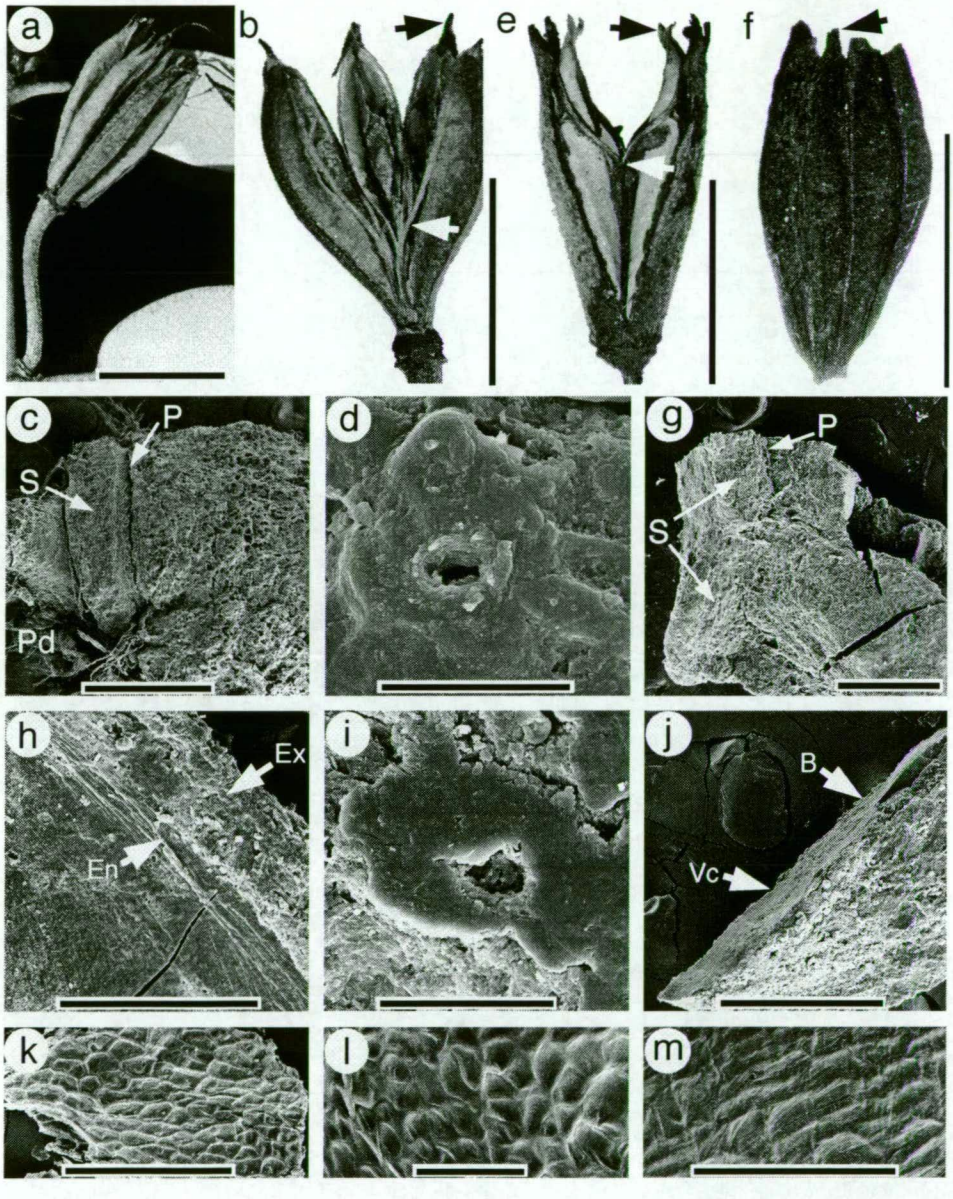
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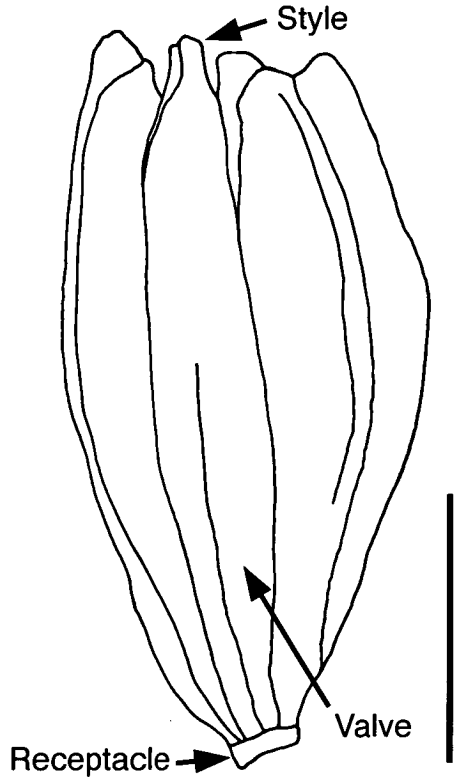
Fig. 5.6. Line drawing of the holotype of *Eucryphia reticulata* R.W.Barnes & G.J.Jord. (Lea-3301; Fig. 5.5.f) from Lea River, north-western Tasmania. Note the attached receptacle and the single terminal style preserved on a single valve. Scale bar = 5 mm.


Style
Valve
Receptacle

endocarp (Dickison 1978; Fig. 5.5.b). The endocarp and exocarp are fused but remain distinct (see Figs 5.2.f and 5.5.b). The endocarp is thin and papery while the exocarp is strongly lignified. At fruit maturity the receptacle retains the scars where the sepals were attached and the insertion point of the petals, immediately adjacent to the sepal scars (Fig. 5.5.c). The exocarp is covered in simple trichome bases (Fig. 5.5.d) which vary in density among the extant species (see also Forster and Hyland 1997). The presence of a central vascular connective between the carpels for at least part the length of the capsule and persistent apical styles upon capsule maturity are also features in other Cunoniaceae, such as *Geissois* (Fig. 5.5.e), *Lamanonia, Ackama* and *Spiraeopsis* (see also Godley 1983), however *Eucryphia* is unique in the large number of valves per capsule.

The fossil *Eucryphia* capsule is complete with all eight valves still attached (Figs 5.5.f and 5.6). Scars where the sepals were attached and probable petal insertion point are preserved on the receptacle at the base of the capsule (Fig. 5.5.g). The endocarp and exocarp are distinct, with the endocarp being thin and glabrous (Fig. 5.5.h) while the exocarp is thicker, probably lignified and is covered in small trichome bases similar to those present on the exocarp of extant species, for example *E. lucida* (Fig. 5.5.i cf. Fig. 5.5.d). The remnants of a vascular connective fused to the inner endocarp is preserved which splits at the valve suture, and is identical to the type of capsule dehiscence in the extant species (Fig. 5.5.j cf. Fig. 5.5.b). Some valves contained well preserved seed coats which have a highly reticulate and indented surface, similar to the reticulate seed coat of extant *Eucryphia* species (Fig. 5.5.k cf. Fig. 5.5.l-m). A reticulate seed coat is also present in other Cunoniaceae, such as *Geissois* and *Lamanonia* (Dickison 1984; Hufford and Dickison 1992).

The fossil capsule has more valves than extant *E. milliganii* (4-5), *E. lucida* (5-7) and *E. moorei* (5-7) and is larger in size than the capsules of *E. wilkiei* and *E. jinksii*, which both have capsules of 7-9 valves. The capsule is most similar to those present in the two South American species *E. glutinosa* and *E. cordifolia* based on size and the number of valves but the seed coat of the fossil is more strongly reticulate and deeply indented than any living species. The fossil capsule could be conspecific with the fossil leaf species described from this or another deposit but in the absence of any organic connection to a leaf or leaf fragment it is assigned to a new species, *Eucryphia reticulata.*

The single leaf fragment extracted from this locality (Lea-3302) is interpreted to be a leaflet derived from a compound leaf as it is highly falcate, especially in the upper section (Fig. 5.7.a). The leaflet has a cuneate base and entire margin. The apex is not

Figs 5.7.a-h. Holotype of *Eucryphia leaensis* R.W.Barnes & G.J.Jord. (Lea-3302) from Lea River, north-western Tasmania.

Fig. 5.7.a. Macrofossil. Note falcate leaf shape. Scale bar = 5 mm.

Figs 5.7.b-h. Light micrographs of the abaxial cuticle.

Fig. 5.7.b. Stoma (centre) showing brachyparacytic subsidiary cell arrangement (arrows indicate the positions of subsidiary cells). Scale bar = 30 µm.

Fig. 5.7.c. Stomata occur in weak areoles and are obscured by well developed peltiform extensions. Scale bar = 100 µm.

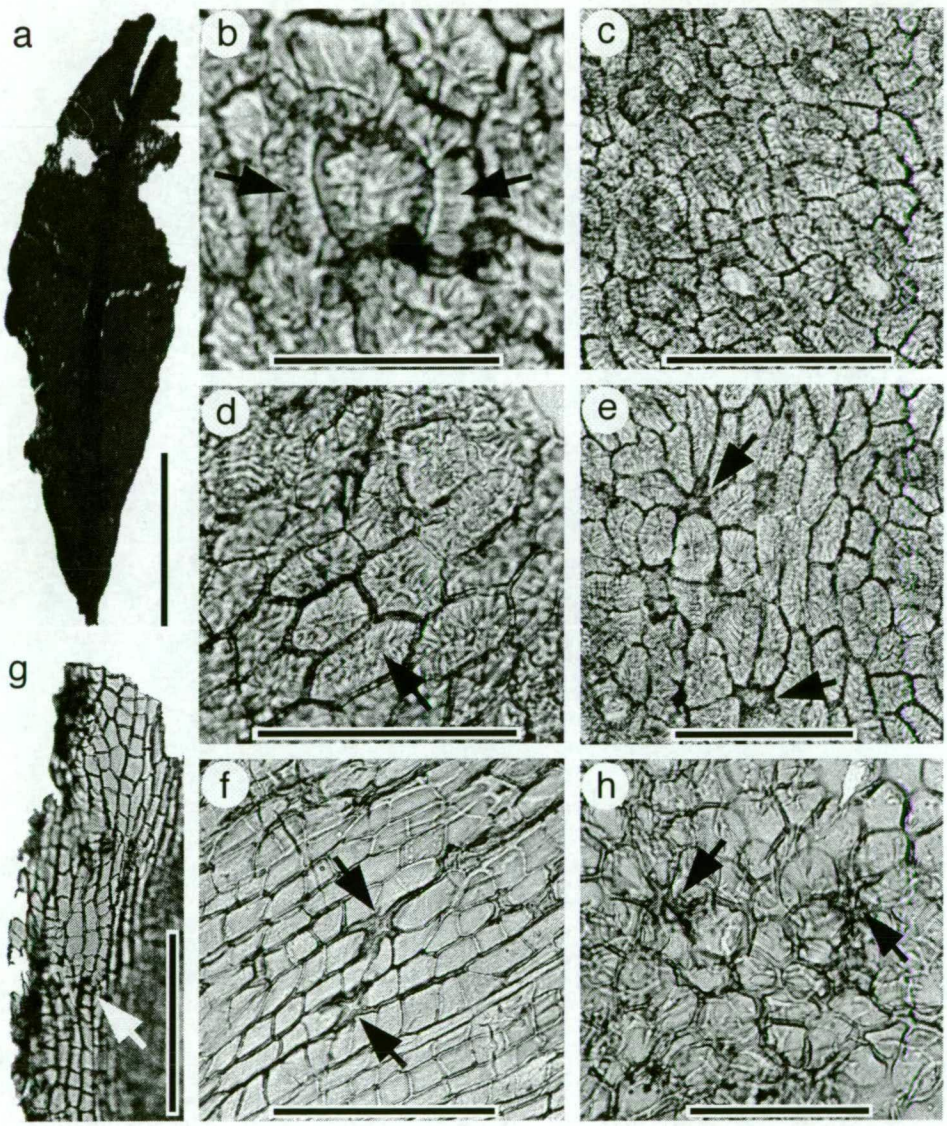
Fig. 5.7.d. Epidermal cells on a minor vein showing peltiform extensions (arrow). Scale bar = 50 µm.

Fig. 5.7.e. Unicellular hair bases on a minor vein (arrows). Scale bar = 80 µm.

Fig. 5.7.f. Apical midrib showing unicellular hair bases (arrows) and a lack of peltiform extensions. Scale bar = 100 µm.

Fig. 5.7.g. Leaf margin showing sparse hair bases (arrow). Scale bar = 250 µm.

Fig. 5.7.h. Light micrograph of the adaxial cuticle showing isodiametric epidermal cells and unicellular hair bases (arrows). Scale bar = 70 µm.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preserved in its entirety but was probably acute in shape. It is not possible to determine if the species was polymorphic for leaf margin form as only a single leaflet is preserved. Secondary venation is brochidodromous with only few lateral vein pairs. Stoma have a brachyparacytic subsidiary cell arrangement (Fig. 5.7.b) and occur in weakly defined areoles (Fig. 5.7.c). The abaxial lamina has well developed peltiform extensions (Fig. 5.7.c-d) that also extend onto the minor veins (Fig. 5.7.e) but are absent from the entire length of the midrib (Fig. 5.7.f). Unicellular trichome bases are present on the minor veins and midrib (Fig. 5.7.e-f) and are surrounded by 5-6 epidermal cells with a slight thickening of the inner surface (e.g. Fig. 5.7.e). The leaf margin is sparsely pubescent (Fig. 5.7.g). The epidermal cells on the adaxial surface are isodiametric and there are numerous trichome bases preserved (Fig. 5.7.h).

On the basis that the leaflet is from a compound leaf, and that the margin is entire, it is most similar to the fossil taxon *E. aberensis* and the three extant species *E. moorei, E. wilkiei* and *E. jinksii*. However, the fossil leaf differs from these species as it has a pubescent abaxial lamina (nearly glabrous in *E. aberensis*) and sparsely pubescent margins (numerous hairs in *E. moorei, E. wilkiei* and *E. jinksii*). Although these features distinguish it from these taxa it may be derived from the same parent plant as *E. reticulata*, but in the absence of an organic connection it is assigned to a new species, *Eucryphia leaensis.*

5.3.2 Wilson's Creek, central Tasmania

The specimen WC-33 (Fig. 5.8.a) is the only fossil *Eucryphia* leaf extracted from Wilson's Creek. The leaf is incomplete, approximately 70 mm long and 26 mm wide at the widest point without the apex preserved (Fig. 5.8.a). The base is acute and symmetrical, so it is not possible to determine if it is a simple leaf, or a terminal leaflet, or a symmetrical lateral leaflet. The margin is irregularly serrate with a prominent, apically directed mucronate extension on each tooth apex (Fig. 5.8.a), similar to those in extant *E. cordifolia* (Fig. 5.3.e) and *E. glutinosa* (see Fig. 5.3.f).

Stomata are restricted to the abaxial surface and have a brachyparacytic subsidiary cell arrangement (Fig. 5.8.b). Cuticular peltiform extensions are well developed on the abaxial lamina (Fig. 5.8.c-d), poorly developed on minor veins (Fig. 5.8.d) and are entirely absent from the midrib (Fig. 5.8.e). Grooves lead in to the cuticular extensions (Fig. 5.8.f). Trichome bases are simple, surrounded by 5-7 radially arranged epidermal cells (Fig. 5.8.g) and are restricted to the midrib and higher veins on both surfaces. Hydathodes are also present on the major abaxial veins (Fig. 5.8.h)

Figs 5.8.a-h. Holotype of *Eucryphia mucronata* R.W.Barnes & G.J.Jord. (WC-33) from Wilson's Creek, central Tasmania.

Fig. 5.8.a. Macrofossil showing mucronate tooth apices (arrows). Scale bar = 10 mm.

Figs 5.8.b-h. Light and scanning electron micrographs of the abaxial cuticle of WC-33.

Fig. 5.8.b. Inner surface of a stoma showing brachyparacytic subsidiary cell arrangement (arrows indicate the positions of subsidiary cells). Scale bar = 25 µm.

Figs 5.8.c-e. Outer surface showing the distribution of cuticular peltiform extensions.

Fig. 5.8.c. Well developed lamina extensions.

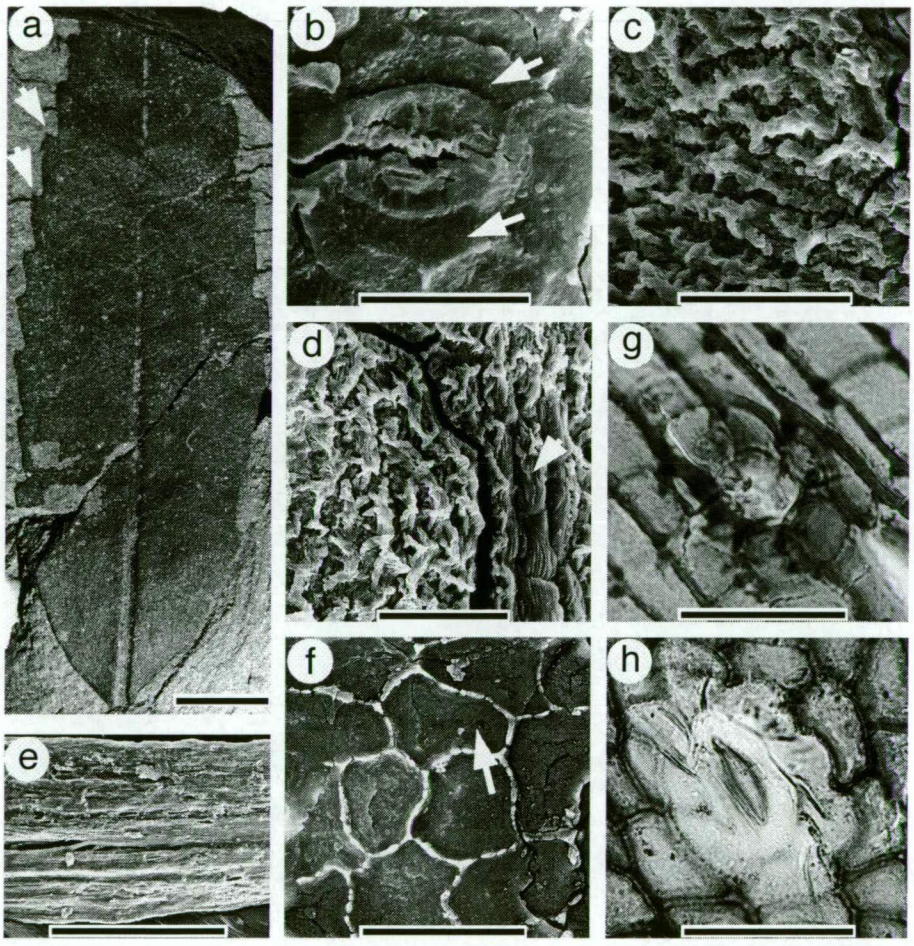
Fig. 5.8.d. Vein (arrow) showing weak extension development. Scale bar for both = 50 µm.

Fig. 5.8.e. Apical midrib with no extensions. Scale bar = 150 µm.

Fig. 5.8.f. Inner surface showing groove in epidermal cell (arrow). Scale bar = 40 µm.

Fig. 5.8.g. Unicellular hair base on midrib with radially modified epidermal cells. Scale bar = 50 µm.

Fig. 5.8.h. Hydathode on vein. Scale bar = 30 µm.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and the midrib.

The fossil taxon described here has several features characteristic of evergreen *Eucryphia* species and include a brachyparacytic subsidiary cell arrangement (Fig. 5.8.b), dense abaxial peltiform extensions (e.g. Fig. 5.8.d) and simple unicellular trichome bases with radially arranged slightly modified epidermal cells (Fig. 5.8.g) on both leaf surfaces. Like the leaves of the two South American species, *E. cordifolia* and *E. glutinosa*, and the juvenile leaves of *E. moorei, E. lucida* and *E. milliganii*, the fossils' margins have several irregular mucronate teeth. However, the fossil differs from *E. glutinosa* by the presence of well developed cuticular peltiform extensions and from *E. cordifolia* by the presence of an acute leaf base (Fig. 5.8.a cf. 5.3.e). The fossil is most similar to the fossil taxa *E. falcata* from Lake Bungarby and *E. aberensis* from Loch Aber but differs in having well developed abaxial peltiform extensions (unlike *E. falcata*) and trichomes on the abaxial lamina (unlike *E. aberensis*) so it is assigned to a new species, *Eucryphia mucronata.*

5.3.3 Loch Aber, north-eastern Tasmania

Numerous leaves and leaf fragments of *E. aberensis* were extracted from Loch Aber sediment and examined in conjunction with those from the study of Hill (1991*a*). Hill (1991*a*) suggested that the macrofossils of *E. aberensis* may represent single leaves or leaflets from a compound leaf. The latter hypothesis is supported by both the discovery of two *Eucryphia* leaflets with an organic connection preserved (Figs 5.9.a and 5.10) and the presence of leaflets with either an asymmetrical (Fig. 5.9.b) or symmetrical leaf base (Fig. 5.9.c). The leaflets either have entire margins (Fig. 5.9.c-d) and brochidodromous venation (Fig. 5.9.d) or are serrate, at least in the apical region (Fig. 5.9.e). A single leaflet apex was located and is attenuate in shape (Fig. 5.9.f). The variation in leaf form may be interpreted as representing two *Eucryphia* species. However, it is more probable that *E. aberensis* was polymorphic for leaf margin form given that all leaflets examined possessed well developed peltiform cuticular extensions (Fig. 5.9.g-h), a brachyparacytic subsidiary cell arrangement (Fig. 5.9.g), a glabrous abaxial lamina (Fig. 5.9.h) and sparse unicellular trichome bases on the midrib (Fig. 5.9.i) and margins (Fig. 5.9.j).

Peltiform cuticular extension development and trichome distribution in *E. aberensis* is similar to that observed in extant *E. lucida* and *E. milliganii* ssp. *milliganii*, however these species have leaves with entire margins and are predominantly simple. The shape and size of the serrations in *E. aberensis* are similar to those in *E. mucronata*

Figs 5.9.a-j. *Eucryphia aberensis* from Loch Aber, north-eastern Tasmania.

Fig. 5.9.a. Incomplete compound leaf (LA-222) with leaflets still attached (arrow indicates basal attachment).
Fig. 5.9.b. Probable leaflet (LA-239) with asymmetrical base (arrow).
Fig. 5.9.c. Entire margin leaf or leaflet (LA-245) with symmetrical base.
Fig. 5.9.d. LA-245 showing brochidodromous secondary venation.
Fig. 5.9.e. LA-229 showing apical serrations (arrows). Scale bars for Figs 5.9.a-e = 10 mm.
Fig. 5.9.f. Attenuate apex (LA-227). Scale bar = 1 mm.

Figs 5.9.g-j. Light micrographs of the abaxial cuticle.
Fig. 5.9.g. LA-222 showing stoma with brachyparacytic subsidiary cell arrangement (arrows indicate subsidiary cells) and well developed peltiform extensions. Scale bar = 100 μm.
Fig. 5.9.h. Secondary vein of LA-212 showing well developed peltiform extensions (arrow). Scale bar = 100 μm.
Fig. 5.9.i. Apical region of midrib of (LA-227) showing hair bases and no peltiform extensions. Scale bar = 250 μm.
Fig. 5.9.j. Sparse unicellular hair bases (arrow) on leaf margin (LA-235). Scale bar = 60 μm.

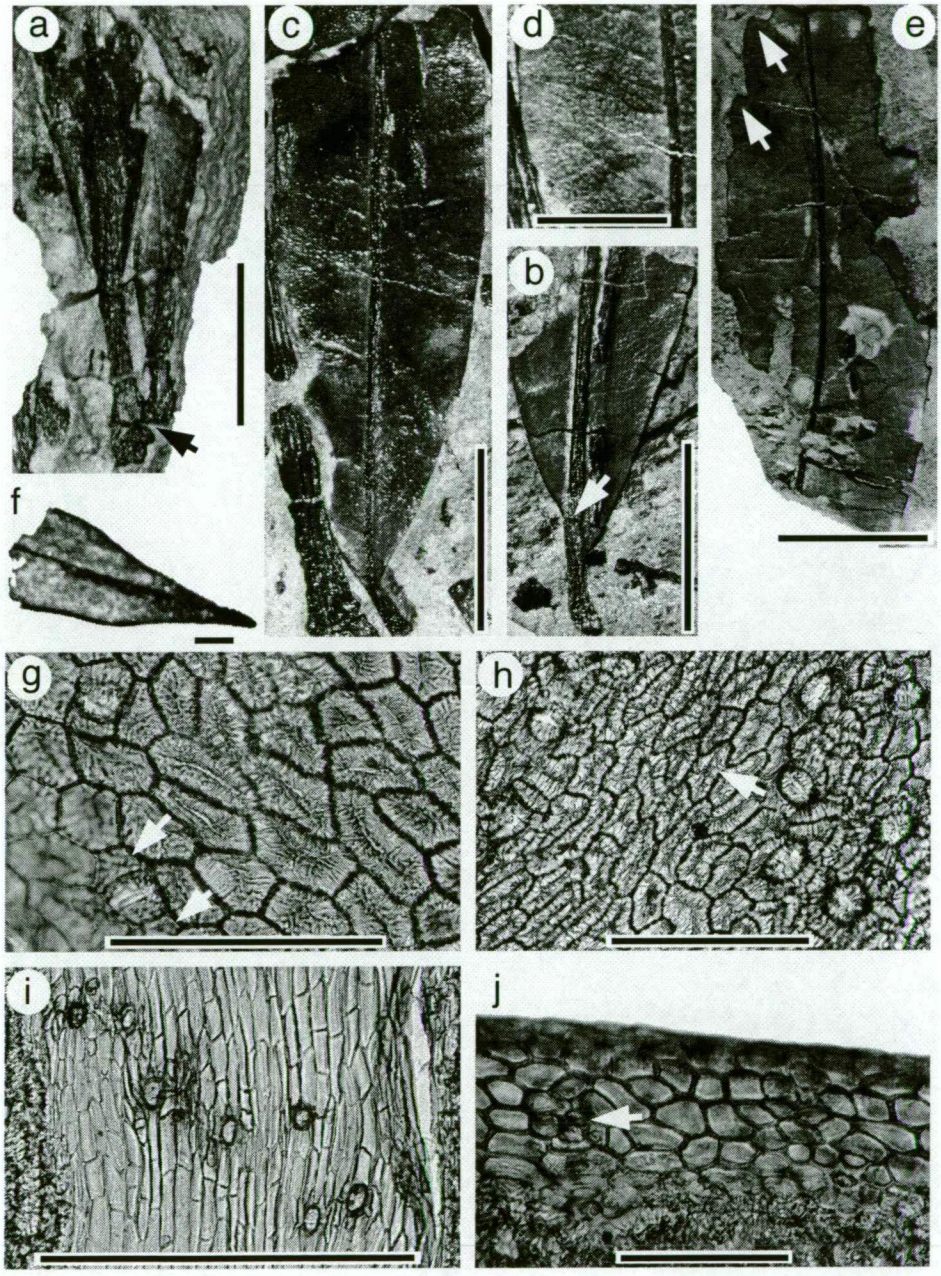
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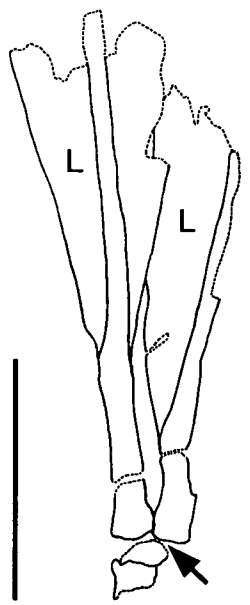
Fig. 5.10. Line drawing of specimen LA-222 (*Eucryphia aberensis*; Fig. 5.9.a) from Loch Aber, north-eastern Tasmania. Note that the specimen represents a compound leaf formed by two leaflets (L) attached at the base (arrow). Scale bar = 10 mm.


L
L

(Fig. 5.9.e cf. Fig. 5.8.a) but differs from this species, and all other fossil leaf species, in possessing a glabrous abaxial lamina. Therefore, the specific status of *E. aberensis* is supported. An emended diagnosis is presented here to include the presence of compound leaves consisting of leaflets with entire or serrate margins.

5.3.4 Little Rapid River, north-western Tasmania

The leaf fragments examined from this locality are consistent with having been part of a compound leaf as the leaf bases are either symmetrical (Fig. 5.11.a) or asymmetrical (Fig. 5.11.b). Leaflets either have an entire margin (Fig. 5.11.c-d) or are serrate, at least in the apical region (Fig. 5.11.e-f), with tooth apices similar in shape to those of *E. aberensis* from Loch Aber (cf. Fig. 5.9.e). As with *E. aberensis* from Loch Aber, the variation in leaf margin form is interpreted here as being consistent with variation within a single species, especially since the cuticle morphology of all the specimens examined is identical. In particular, all leaflets possess a brachyparacytic subsidiary cell arrangement (Fig. 5.11.g) and well developed cuticular peltiform extensions that occur on minor veins (Fig. 5.11.i) but are absent from the midrib (Fig. 5.11.h). Simple unicellular trichome bases occur on the abaxial midrib (Fig. 5.11.h) but are absent from the abaxial lamina and veins (Fig. 5.11.i). Marginal trichome bases are sparse (Fig. 5.11.j) and the adaxial surface is glabrous (Fig. 5.11.k). On the basis of leaflet shape and form, and foliar hair distribution, the fossils differ from all extant and fossil taxa except for *E. aberensis* so are assigned to that species here.

The fossil capsule extracted from this locality is not complete. The capsule is poorly preserved as two attached valves, with the remnants of a terminal style on a single valve only (Figs 5.12.a-c). One valve is prominently keeled (Fig. 5.12.c). It is not possible to determine the exact number of valves that would have formed the capsule, but it would have been more than six based on the dimensions of the preserved valves. This excludes all other Cunoniaceae genera with dehiscent capsules as these all possess two to five valves (e.g. Dickison 1984; Hufford and Dickison 1992). The receptacle, which was preserved in *E. reticulata* (Fig. 5.5.g), is absent from this specimen but the valves do possess a distinct endo- and exocarp (Fig. 5.12.a-b) and the remnants of a vascular connective fused to the inner endocarp (Fig. 5.12.d), similar to that in extant *E. lucida* (cf. Fig. 5.5.b) and fossil *E. reticulata* (cf. Fig. 5.5.j). The exocarp is generally glabrous (Fig. 5.12.e) except for occasional unicellular trichome (Fig. 5.12.f) which are similar to those in extant *E. lucida* (cf. Fig. 5.5.d) and extinct *E. reticulata* (cf. Fig. 5.5.i). No seed coats were located in the dehisced valves.

Figs 5.11.a-k. *Eucryphia aberensis* from Little Rapid River, north-western Tasmania.

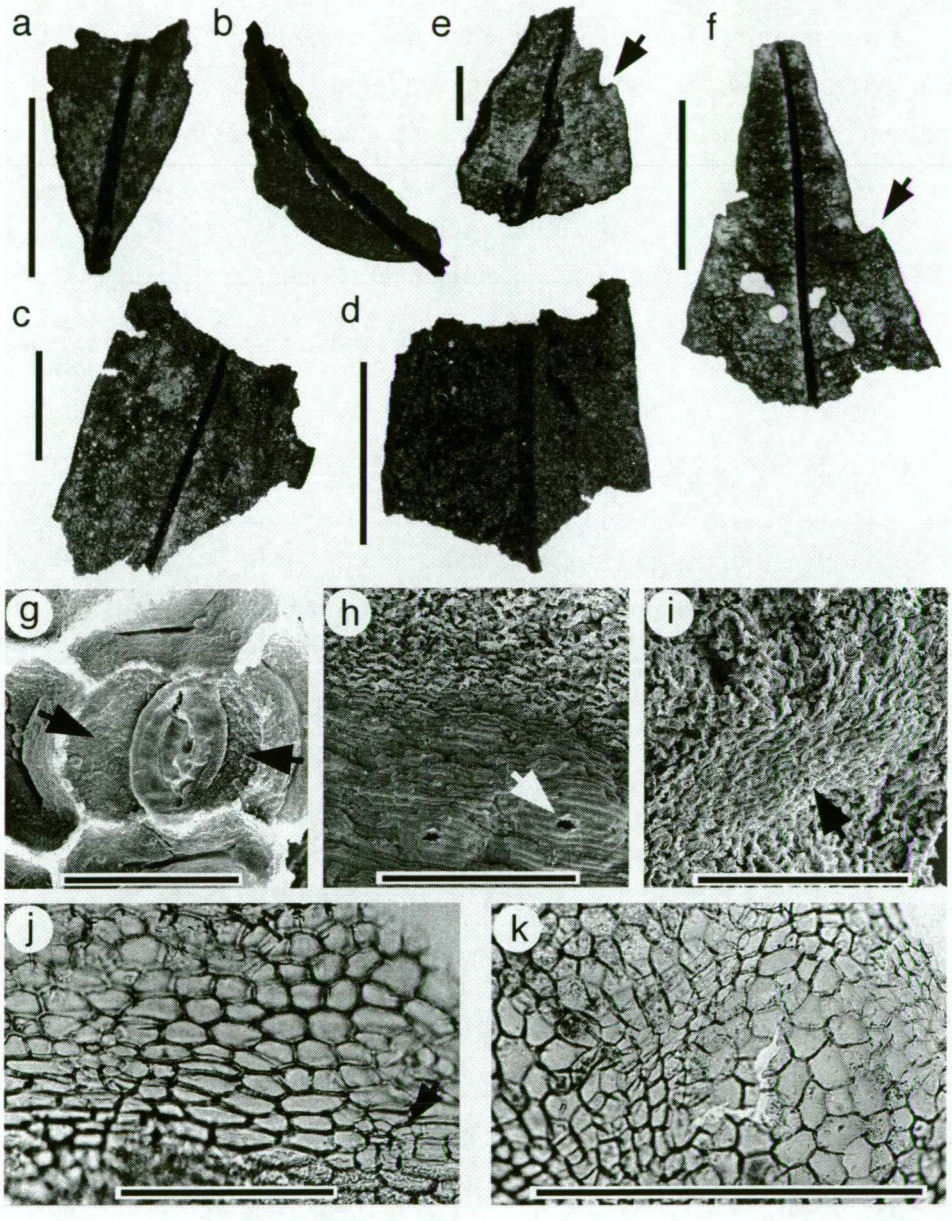
Fig. 5.11.a. Leaf or leaflet with symmetrical base (LRR1-4057).
Fig. 5.11.b. Leaflet with asymmetrical base (LRR1-4010). Scale bar for both = 5 mm.

Figs 5.11.c, d. Leaflets with entire margins. **Fig. 5.11.c.** LRR1-4024. **Fig. 5.11.d.** LRR1-4030. Scale bar for both = 5 mm.

Figs 5.11.e, f. Leaflets with serrations (arrows). **Fig. 5.11.e.** LRR1-4027. Scale bar = 1 mm. **Fig. 5.11.f.** LRR1-4053. Scale bar = 5 mm.

Figs 5.11.g-i. Scanning electron micrographs of the abaxial cuticle (LRR1-4010).
Fig. 5.11.g. Inner surface of stoma showing brachyparacytic subsidiary cell arrangement (arrows). Scale bar = 20 µm.
Fig. 5.11.h. Outer surface showing sparse unicellular hair bases on midrib (arrow) and well developed peltiform extensions on lamina. Scale bar = 200 µm.
Fig. 5.11.i. Minor vein (arrow) showing the presence of peltiform extensions. Scale bar = 200 µm.

Figs 5.11.j, k. Light micrographs of the cuticle of specimen LRR1-4010.
Fig. 5.11.j. Sparse unicellular hair bases (arrow) on leaf margin. Scale bar = 100 µm.
Fig. 5.11.k. Adaxial surface. Scale bar = 250 µm.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Figs 5.12.a-f. Incomplete fossil capsule of *Eucryphia* sp. 'LRR1' (LRR1-4046) from Little Rapid River, north-western Tasmania.

Fig. 5.12.a. Macrofossil in side view. Note the single remnant apical style (black arrow) and the distinction between the exocarp and endocarp (white arrow).

Fig. 5.12.b. Line drawing of the incomplete capsule in figure 5.12.a showing the two attached valves, one with a remnant terminal style. The exocarp and endocarp are clearly distinct and a ventral suture is present on one valve.

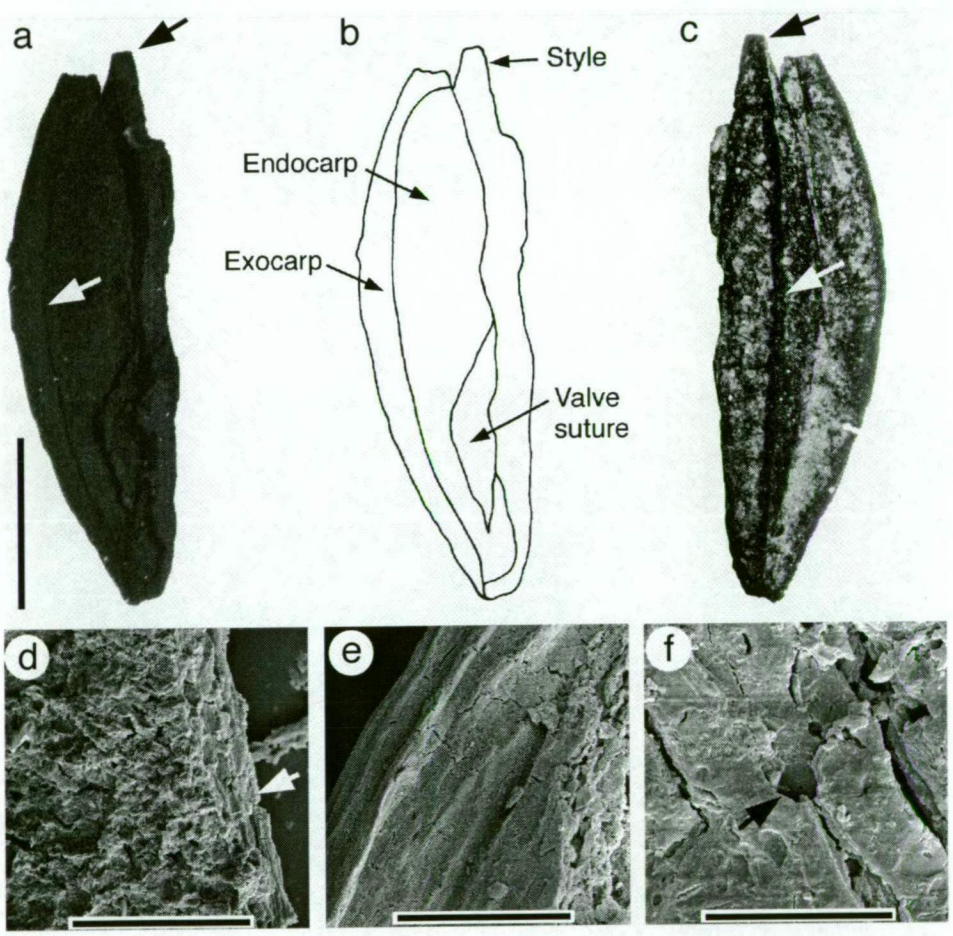
Fig. 5.12.c. Macrofossil showing the outer exocarp of each valve. Note the remnant terminal style (black arrow) and a prominent keel (white arrow) on a single valve. Scale bar for Figs 5.11.a-c = 5 mm.

Figs 5.12.d-f. Scanning electron micrographs of the endocarp and exocarp.

Fig. 5.12.d. Side view of a valve showing the remnants of a central vascular connective (arrow) fused to the inner valve. Scale bar = 100 µm.

Fig. 5.12.e. Outer exocarp showing relatively glabrous surface with well preserved cellular outline. Scale bar = 200 µm.

Fig. 5.12.f. Unicellular hair base on exocarp (arrow). Scale bar = 20 µm.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The incomplete capsule has features characteristic of *Eucryphia* (multiple boat-shaped valves, terminal apical style, vascular connective fused to the inner endocarp and a distinct endocarp and exocarp that is pubescent) but because the number of valves is unknown the specimen cannot be assigned with confidence to either an extant or extinct genus. It is possible that the capsule is conspecific with *E. aberensis,* which is represented by leaves in both this and the Loch Aber deposit, but cannot be confirmed due to the lack of any organic connection. As additional specimens need to be located and examined to determine the affinities of the fossil capsule it will be referred to as *Eucryphia* sp. 'LRR1'.

5.3.5 Regatta Point, western Tasmania

The specific epithet of the Early Eocene species *Eucryphia microstoma* refers to the small size of the stomata compared to those in other extinct and extant species (see Hill 1991*a*). The subsidiary cell arrangement of *E. microstoma* is always brachyparacytic according to Hill (1991*a*), which is the common condition within other fossil and all extant species (e.g. *E. jinksii*, Fig. 5.4.d). The unicellular trichome bases have 5-7 radially modified basal epidermal cells (see figures in Hill 1991*a*), however the trichome base does not conform to the 'peg' type, as described by Dilcher (1974), that occurs in all extant and extinct *Eucryphia* species. In *E. microstoma* there is cuticle present at the base of the trichome, creating a seal where the trichome cell could not have been part of the epidermis. This is contrast to all other *Eucryphia* species, and indeed most other Cunoniaceae genera such as *Geissois, Ceratopetalum* (Chapter 3 this study) and *Callicoma* (Chapter 4 this study) where the trichome cell would have been part of the epidermal layer. Therefore, *E. microstoma* is probably not *Eucryphia* but, as its correct taxonomic affinities are unknown, it will remain in the genus until it is formally reassigned to another taxon. It may be argued that the fossil should be assigned to the leaf form genus *Phyllites* or a similar genus to avoid any possible future confusion with the *Eucryphia* fossil record. However, by doing this it simply generates generic and/or specific names that may then also become redundant, which then only confuses this situation further.

The Early Pleistocene *Eucryphia* macrofossils from Regatta Point have received appreciable attention, particularly from Hill (1991*a*), Taylor (1993) and Taylor and Hill (1996). The fossils examined by Hill (1991*a*) had a glabrous abaxial surface except for a few scattered hairs along the midrib. This pattern was considered by Hill (1991*a*) to be at one end of the variability in *E. milliganii* and is identical to that present in *E.*

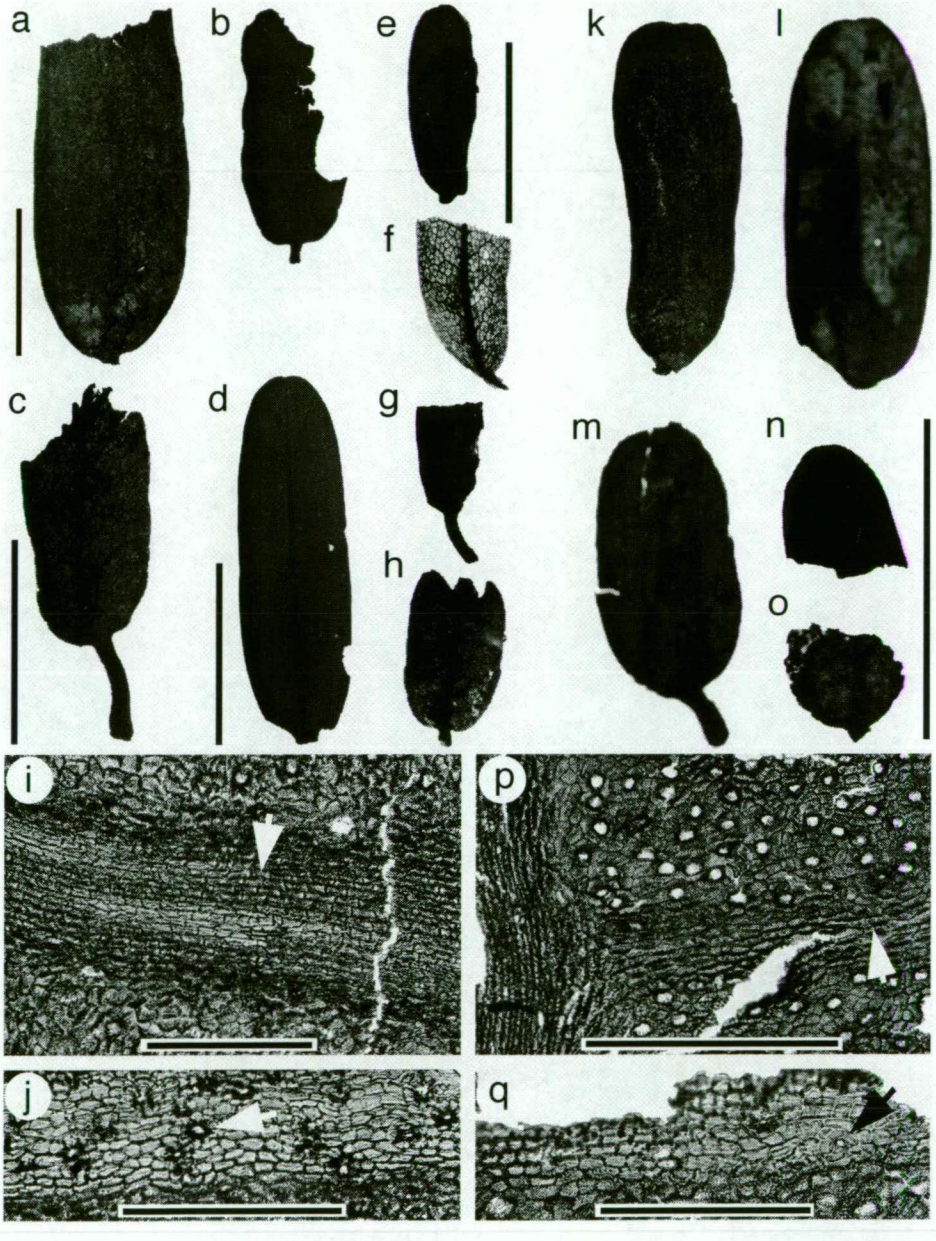
Figs 5.13.a-q. Fossil *Eucryphia lucida* and *E. milliganii* ssp. *milliganii* leaves and abaxial cuticle from Early Pleistocene sediments at Regatta Point, western Tasmania.

Figs 5.13.a-h. *Eucryphia lucida* macrofossils. **Fig. 5.13.a.** RPU-4670. **Fig. 5.13.b.** RPU-4650. Scale bar for Figs 52, 53 = 10 mm. **Fig. 5.13.c.** RPU-4657. **Fig. 5.13.d.** RPU-4673. Scale bars for Figs 54, 55 = 10 mm. **Fig. 5.13.e.** RPU-4686. **Fig. 5.13.f.** RPU-4718. **Fig. 5.13.g.** RPU-4687. **Fig. 5.13.h.** RPU-4666. Note apical serrations. Scale bar for Figs 56-59 = 10 mm.

Figs 5.13.i, j. Light micrographs of the abaxial cuticle of *Eucryphia lucida* (RPU-4650).
Fig. 5.13.i. Abaxial surface showing glabrous midrib (arrow) and lamina.
Fig. 5.13.j. Leaf margin showing dense hair bases (arrow). Scale bar for both = 200 µm.

Figs 5.13.k-o. *Eucryphia milliganii* ssp. *milliganii* macrofossils. **Fig. 5.13.k.** RPU-4660. **Fig. 5.13.l.** RPU-4655. **Fig. 5.13.m.** RPU-4653. **Fig. 5.13.n.** RPU-4707. **Fig. 5.13.o.** RPU-4698. Scale bar for Figs 62-66 = 10 mm.

Figs 5.13.p, q. Light micrographs of the abaxial cuticle of *Eucryphia milliganii* ssp. *milliganii* (RPU-4655).
Fig. 5.13.p. Abaxial surface showing glabrous midrib (left), lamina and vein (arrow). Scale bar = 300 µm.
Fig. 5.13.q. Leaf margin showing a single hair base (arrow). Scale bar = 200 µm.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lucida so the fossils were assigned to *E.* aff. *milliganii*. Hill (1991*a*) also noted that the fossil leaves were small compared to those of extant *E. lucida* but were well within the size range of extant *E. milliganii*. This identification was accepted by Taylor and Hill (1996) in a phylogenetic study of the fossil species described at that time.

A re-examination of the *Eucryphia* macrofossils extracted during previous studies (e.g. Jordan 1992) indicated that the fossil leaves fall into two distinct groups based on differences in foliar hair distribution and density. In particular, all macrofossils are identical in foliar hair distribution and density to that observed within either extant *E. lucida* (Hill 1991*a*; Taylor 1993; Taylor and Hill 1996) or the subspecies of *E. milliganii* (Barnes *et al.* 2000). *Eucryphia lucida* has a glabrous abaxial surface with dense hairs along the leaf margins (Hill 1991*a*; Taylor 1993). Barnes *et al.* (2000) have shown that there are two subspecies of *E. milliganii* based on leaf shape and leaf pubescence. *Eucryphia milliganii* ssp. *milliganii* has oblong leaves with a glabrous abaxial surface and sparse trichomes along the margins while leaves of *E. milliganii* ssp. *pubescens* are ovate to elliptic with a pubescent abaxial lamina and margins.

Numerous whole and fragmented large (Fig. 5.13.a-d) and small leaves (Fig. 5.13.e-h) of fossil *E. lucida* were identified. Leaf bases are symmetrical (e.g. Fig. 5.13.b) and therefore probably represent simple leaves. However, even in trifoliate leaves of extant *E. lucida* it is very difficult to differentiate between lateral and terminal leaflets. The single leaf with apical serrations (Fig. 5.13.h) probably represents a juvenile leaf as rosid teeth are common in the first few leaves of seedlings (Hill 1991*a*) and occasionally on coppice growth (R. W. Barnes pers. obs.). The abaxial cuticle in all cases is glabrous (Fig. 5.13.i), with the exception of a few trichome bases along the midrib, and the margins preserve densely arranged trichome bases (Fig. 5.13.j). The leaves described here conform to the pattern of foliar hair distribution in extant *E. lucida* and, although variable in size, occur within the size range of the extant species, so are assigned to *E. lucida* here.

The fossils leaves and leaf fragments of *E. milliganii* ssp. *milliganii* (Fig. 5.13.k-o) are smaller and less common than those of *E. lucida*. Leaves are linear to oblong in shape and have an emarginate apex (Fig. 5.13.k-l). The abaxial cuticle is glabrous (Fig. 5.13.p), with scarce to no trichome bases on the leaf margin (Fig. 5.13.q). On the basis of leaf shape, a glabrous abaxial lamina and sparsely pubescent margins the leaves are assigned to the extant species *E. milliganii* ssp. *milliganii* here.

The slightly younger Early-Middle Pleistocene clasts examined by Jordan *et al.* (1995) contain dispersed cuticle of *Eucryphia* but no intact or fragmented mummified leaves or

leaf impressions. Given the age of the clasts and the occurrence of the extant Tasmanian species in the older sediments at this locality, it is extremely unlikely that the cuticle represents an extinct species. On this basis, the absence of abaxial trichomes on the lamina or veins of the cuticle excludes any affinity to extant *E. milliganii* ssp. *pubescens*, which has been suggested by Barnes *et al.* (2000) to have evolved within southern Tasmania and may have never occurred in western Tasmania. The cuticle cannot, however, be distinguished from extant *E. lucida* or *E. milliganii* ssp. *milliganii*.

5.3.6 Regency Formation, western Tasmania

The macrofossils of *Eucryphia* from the Regency Formation are conspecific with the two extant Tasmanian species *E. lucida* and *E. milliganii* on the basis of leaf shape and foliar hair distribution, which is in accordance with Fitzsimons *et al.* (1990), Jordan (1992) and Taylor (1993). More specifically, the majority of the leaf macrofossils are typical of *E. milliganii* ssp. *milliganii* as they are oblong to elliptic in shape and have a glabrous abaxial lamina and nearly glabrous margins (see also Taylor 1993).

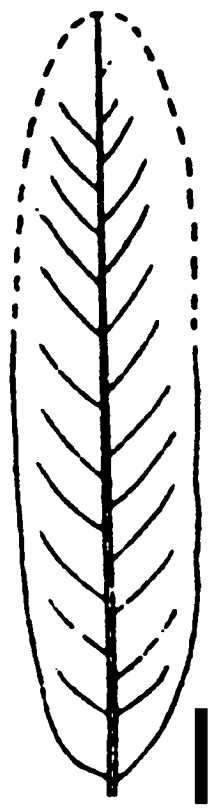
5.3.7 Leven River, north-western Tasmania

Some fragments of dispersed cuticle (Lev-100) located in the Leven River sediment are typical of *Eucryphia* (abaxial peltiform extensions, a brachyparacytic subsidiary cell arrangement and simple unicellular trichome bases); however, no whole or fragmented macrofossils were located. This cuticle could not be distinguished from most evergreen extant or fossil species. The presence of well developed peltiform extensions, a groove leading into the epidermal cells and trichome bases restricted to the midrib suggests an affinity to the extant Australian species *E. lucida* and *E. milliganii* ssp. *milliganii* and the fossil taxon *E. aberensis*. As leaves or leaf fragments need to be examined to enable an identification to the species level the cuticle will be referred to as *Eucryphia* sp. 'Leven'.

5.3.8 Pitfield, Victoria

The description and illustration of the single specimen described as *Eucryphia gregorii* by Deane (1902*c*; Fig. 5.14) does not contain enough information for it to be assigned to *Eucryphia* with any level of confidence. However, it must be noted that based on

Fig. 5.14. Line drawing of *Eucryphia gregorii* described by Deane (1902*c*) from the Pitfield deposit in Victoria. Deane (1902*c*) makes particular note of the numerous lateral veins that lose themselves in the substance of the leaf before finally reaching the margin. The leaf is compared by Deane (1902*c*) to a pinna of extant *E. moorei* and a leaf of *E. lucida*. Scale bar = 10 mm.



the widespread occurrence of *Eucryphia*, both temporally and geographically, it is quite possible that this record is indeed accurate but simply in need of further examination.

5.4 Systematics

The systematics of all the below mentioned fossils are detailed in Barnes and Jordan (2000, Appendix 1).

Eucryphia Cav.

Eucryphia reticulata R.W.Barnes & G.J.Jord., sp. nov. (Figs 5.5.f-k and 5.6)

Diagnosis

Eight valved, septicidally dehiscent capsule. Sparsely pubescent exocarp, hair bases simple, unicellular. Seed coats strongly reticulate and deeply indented.

Holotype: Lea-3301 (single specimen), stored in the School of Plant Science, University of Tasmania.

Type locality

Early Oligocene sediments at Lea River, north-western Tasmania.

Etymology

Named in recognition of the strongly reticulate and deeply indented seed coat.

Eucryphia leaensis R.W.Barnes & G.J.Jord., sp. nov. (Fig. 5.7.a-h)

Diagnosis

Leaf compound. Leaflet margin entire, sparsely pubescent. Well developed abaxial peltiform cuticular extensions. Abaxial midrib and veins pubescent.

Holotype: Lea-3302 (single specimen), stored in the School of Plant Science, University of Tasmania.

Type locality

Early Oligocene sediments at Lea River, north-western Tasmania.

Etymology

Named after the Lea River locality.

Eucryphia mucronata R.W.Barnes & G.J.Jord., sp. nov. (Fig. 5.8.a-h)

Diagnosis

Leaf, base acute. Margins irregularly serrate, tooth apices distinctly mucronate. Well developed abaxial peltiform cuticular extensions. Abaxial lamina, midrib and margins pubescent, hair bases simple, unicellular.

Holotype: WC-33 (single specimen), stored in the School of Plant Science, University of Tasmania.

Type locality

Early Oligocene sediments at Wilson's Creek, near Tarraleah, central Tasmania.

Etymology

Highlights the mucronate tooth apices the length of the leaf.

Eucryphia aberensis R.S.Hill p. 491, figs 31-38. (Figs 5.9.a-j, 5.10, 5.11.a-k)

Emended diagnosis

Leaf compound, leaflets with serrate or entire margins and an attenuate apex. Well developed abaxial peltiform cuticular extensions.

Holotype: LA-013 (housed in the Department of Environmental Biology, University of Adelaide).

Specimens Examined

LA-009, 013, 018, 029, 048, 212, 220, 222, 223-229, 235-236, 238-247. LRR1-4010, 4011, 4013-4014, 4016-4017, 4019-4020, 4022-4028, 4030-4045, 4047-4052, 4057.

Type locality

Middle to Late Eocene sediments at Loch Aber, north-eastern Tasmania.

5.5 Discussion

5.5.1 Extant Species

Eucryphia has an extremely disjunct Southern Hemisphere distribution, with its greatest species diversity within Australia. The genus is characteristic of cool temperate rainforest habitats of the Southern Hemisphere although at least two species, *Eucryphia wilkiei* and *E. jinksii*, occur at lower latitudes in Australia. These are both restricted in their distribution to a very small climatic or habitat niche which has been amenable to their survival (see Fig. 5.1). Forster and Hyland (1997) have suggested that these species are relictual and occupy a very narrow ecological niche within an otherwise unsuitable climate. This is especially the case for *E. wilkiei* which occurs on a cool, upland mountain plateau surrounded by sub-tropical to tropical rainforest. Although these latter species do occur at warm temperate or sub-tropical latitudes, their higher altitude habitats are such that the climate would be more comparable to higher latitudes where *E. moorei* inhabits.

Biogeographically, the absence of *Eucryphia* from New Zealand is notable, especially given its current geographic range in Australia and South America, the large number of extinct species in the Australian fossil record and the age of the oldest fossil species (*E. falcata*, Late Paleocene). *Eucryphia* may have once occurred in New Zealand but has simply not been recovered as a macrofossil. The modern climate of New Zealand should be able to support at least some extant *Eucryphia* species, so their absence from this land mass may be due to the inability of the genus to disperse there after the breakup of Gondwanaland or it has become extinct there at some stage in the past. Fossils of *Eucryphia* from both New Zealand and South America may provide more information on the palaeobiogeography of the genus.

5.5.2 Macrofossil of *Eucryphia*

The verified *Eucryphia* macrofossil record is represented by two capsules, leaves and leaf fragments (Table 5.4). In total, there are six extinct species of *Eucryphia*, and

Table 5.4. Accepted records of *Eucryphia* macrofossils from south-eastern Australia

Three separate fossiliferous deposits occur at Regatta Point; Early Eocene [A] sediments overlain by glacial outwash that contains clay clasts of Early Pleistocene [C] and Early-Middle Pleistocene [B] age.

Source: [A] this study; [B] Hill 1991*a*; [C] Jordan *et al.* 1995; [D] Fitzsimons *et al.* 1990; [E] Jordan 1992; [F] Jordan *et al.* 1991; [G] Colhoun 1980.

Taxon	Fossil locality	Macrofossil	Geological age
Eucryphia falcata [B]	Lake Bungarby	Leaf compressions	Late Paleocene
E. aberensis [AB]	Loch Aber	Mummified leaf fragments	Middle to Late Eocene
E. aberensis [A]	Little Rapid River	Mummified leaf fragments	Early Oligocene
E. sp. 'LRR1' [A]	Little Rapid River	Incomplete mummified capsule	Early Oligocene
E. mucronata [A]	Wilson's Creek	Leaf compression	?Latest Eocene-Early Oligocene
E. reticulata [A]	Lea River	Mummified capsule	Early Oligocene
E. leaensis [A]	Lea River	Mummified leaf fragment	Early Oligocene
E. sp. 'Leven' [A]	Leven River	Dispersed cuticle	Early Oligocene
E. lucida [A]	Regatta Point	Mummified leaves	Early Pleistocene
E. milliganii ssp. *milliganii* [A]	Regatta Point	Mummified leaves	Early Pleistocene
E. sp. [C]	Regatta Point	Dispersed cuticle	Early-Middle Pleistocene
E. lucida [DEA]	Regency Formation	Mummified leaves	Middle Pleistocene
E. milliganii ssp. *milliganii* [DEA]	Regency Formation	Mummified leaves	Middle Pleistocene
E. sp. [F]	Melaleuca Inlet	Dispersed cuticle	Late Pleistocene
E. lucida [G]	Pieman Dam	Mummified leaves	Late Pleistocene

possibly an additional three species if the cuticle and capsule from Little Rapid River (Early Oligocene) and the cuticle from Leven River are distinct from all other fossil and extant species. Additional vegetative and reproductive macrofossils, preferably with organic connections, will need to be examined from these deposits to confirm this. The identification of fossil *Eucryphia* capsules significantly increases the certainty of the identification of the fossil leaf species to the genus, particularly for those deposits (Lea River and Little Rapid River) that contain both reproductive and vegetative remains.

Eucryphia reticulata (Lea River; Early Oligocene) is the first fossil capsule of *Eucryphia* to be described and has similarities to the extant South American species, *E. glutinosa* and *E. cordifolia* based on the number of valves and overall size. The capsule occurs with a single leaf macrofossil, *E. leaensis*, that probably represents a leaflet from a compound leaf based on its highly falcate shape. The leaflet has an entire margin and may be conspecific with *E. reticulata* but requires an organic connection to confirm this.

The second capsule, *Eucryphia* sp. 'LRR1', is incomplete and is generally too poorly preserved to be assigned to a fossil or extant species but can be placed into the genus with confidence. This capsule may be conspecific with *E. aberensis*, with which it occurs (Little Rapid River), but again this cannot be confirmed because of the lack of an organic connection. *Eucryphia aberensis* is the first fossil *Eucryphia* species to be recorded from more than one locality (Table 5.4; Fig. 5.15) and had evolved prior to the Middle to Late Eocene (Loch Aber) and persisted until at least the Early Oligocene (Little Rapid River). The species had compound leaves formed by serrate and entire margin leaflets, which is not expressed in any of the compound leaves of extant species as these have exclusively entire or serrate margins. In the absence of an organic connection between the leaflet forms it is possible that two species are represented in the single taxon *E. aberensis*, one with serrate margins and the other with entire margins. However, based on the available data from this and other studies (Hill 1991*a*), this is unlikely as micro-morphological characters are indistinguishable between the serrate and entire margin leaflets.

Eucryphia mucronata from Wilson's Creek has an irregularly serrate leaf margin and may represent a simple leaf, terminal leaflet or a lateral leaflet of a compound leaf with a symmetrical base. *Eucryphia mucronata* is unique among the fossil species as it is the only one to possess mucronate tooth apices, which are now restricted to the leaves of the two extant species *E. cordifolia* and *E. glutinosa*.

The *Eucryphia* macrofossils from Regatta Point (Early Pleistocene, RPU) and the Regency Formation (Middle Pleistocene) are conspecific with the extant Tasmanian species *E. lucida* and *E. milliganii* ssp. *milliganii.* Taylor and Hill (1996) suggested that the Early Pleistocene Regatta Point macrofossils, assigned to *E.* aff. *milliganii*, may provide the key to understanding the origin of the two Tasmanian species. However, based on the results of this study, their significance to understanding the origin of the two Tasmanian species is somewhat reduced. Of more significance is the absence of *E. milliganii* ssp. *pubescens* in both deposits, which has been suggested by Barnes *et al.* (2000) to have evolved within southern Tasmania in recent times and therefore may have never occurred in western Tasmania. These fossils therefore support the hypothesis of Barnes *et al.* (2000).

The location of *Eucryphia* macrofossils within southern Tasmania may provide a minimum age for the subspeciation of *E. milliganii*, especially if they belong to *E. milliganii* ssp. *pubescens*. Alternatively, fossil leaves of *E. milliganii* ssp. *milliganii* in southern Tasmania would (i) provide support for a more widespread or different distribution of this subspecies in the past, and (ii) provide evidence that it is possibly the ancestral form to *E. milliganii* ssp. *pubescens*, particularly if macrofossils of this latter subspecies were absent. Unfortunately, the only macrofossil of *Eucryphia* from southern Tasmania is the dispersed cuticle from Late Pleistocene sediments at Melaleuca Inlet which has a glabrous lamina so it is of little assistance in solving this problem as it may equally represent *E. lucida* or *E. milliganii* ssp. *milliganii.*

A significant taxonomic problem arises when assigning the Early Pleistocene Regatta Point *Eucryphia* macrofossils to extant *E. milliganii* ssp. *milliganii.* If the subspeciation of *E. milliganii* occurred as recent as Barnes *et al.* (2000) suggest (i.e. Last Glacial), then it is likely that these macrofossils represent the ancestral form to both subspecies prior to subspeciation, and consequently *E. milliganii* ssp. *pubescens* did not actually exist when the leaves were incorporated into the Regatta Point deposit. Therefore, it is equally valid to assign the macrofossils to *E. milliganii* without any reference to a subspecies. This taxonomic problem cannot be resolved satisfactorily due to the incomplete fossil record and without knowing the exact age of the subspeciation event.

From the study of Hill (1991*a*), the oldest fossil *Eucryphia* species, *E. falcata* from Lake Bungarby, has compound leaves with serrate margins which probably resembles the ancestral form of the genus (see also Taylor and Hill 1996). The assignment of *E. microstoma* from Regatta Point (Early Eocene) is considered in this study to be

inappropriate given the differences in hair structure between the specimen and all extant and fossil species. However, as no alternative generic placement has been identified, the fossil will remain in the genus but will not be discussed in the examination of the evolutionary trends.

5.5.3 Evolutionary Trends Within *Eucryphia*

The revised fossil record of *Eucryphia* indicates that there have been three, probably unrelated, evolutionary trends in leaf morphology; the development of entire leaf/leaflet margins, the development of peltiform cuticular extensions on the abaxial lamina, and leaf simplification (Fig. 5.15). As suggested by Taylor and Hill (1996), the ancestral form in *Eucryphia* probably had compound leaves formed by leaflets with a serrate margin (Fig. 5.15), with leaf form evolving in response to climatic changes during the Cainozoic (e.g. decreasing temperatures and precipitation and increasing seasonality; Quilty 1994), as has been suggested for other families (see Hill 1991*b*, 1994; Hill and Carpenter 1991). The phylogenetic analyses of Cunoniaceae by Bradford and Barnes (manuscript submitted, Appendix 1) support the hypothesis that the ancestor to *Eucryphia* had compound adult leaves with serrate margins.

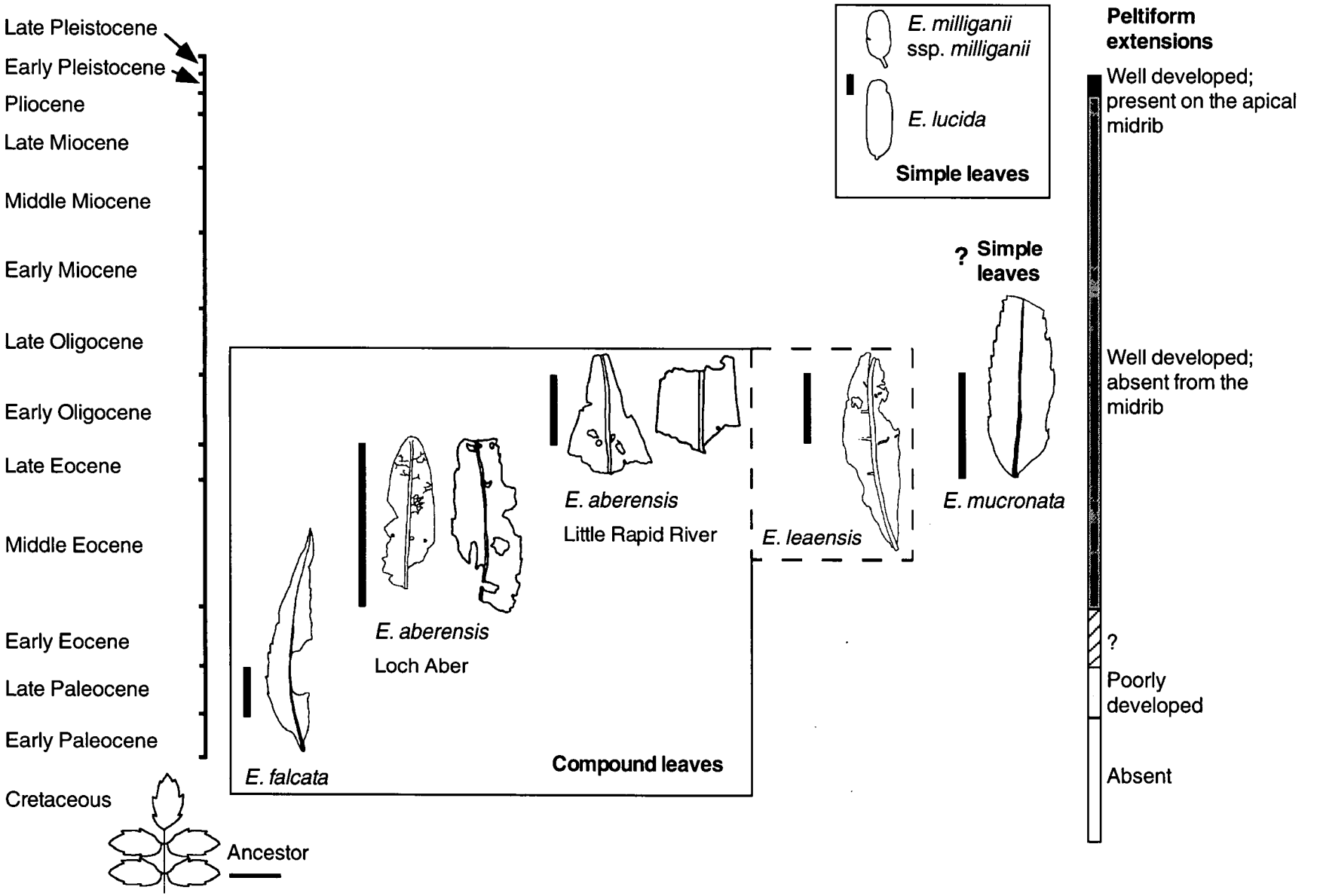
Eucryphia aberensis from Loch Aber shows that entire leaf margins in *Eucryphia* had evolved by the Late Eocene. The variability in leaf form present in *E. aberensis* does not occur in any extant species as all extant species have adult leaves with entire margins except for *E. glutinosa* and *E. cordifolia* which are serrate. Entire margins are the derived condition in the extant Australian species, although their origin may be polyphyletic based on the cladogram of Taylor and Hill (1996) that included the extant and extinct taxa at that time. *Eucryphia moorei, E. lucida* and *E. milliganii* at least exhibit small rosid teeth in the juvenile foliage (Boland *et al.* 1985; Hill 1991*a*) which supports a link to the ancestral form. It is possible that the fossil serrate leaves or leaflets represent the juvenile foliage of a species that had entire margin adult leaves. This is unlikely given the large number of serrate margin leaflets preserved within each deposit, which is often higher than those with entire margins.

The fossil evidence also suggests that the evolution of entire leaf margins postdates, and is independent of, the origin and development of peltiform cuticular extensions (Fig. 5.15). The extensions are poorly developed in *E. falcata* (serrate) but are well developed in *E. mucronata* (serrate), *E. aberensis* (serrate/entire), *E. leaensis* (entire) and the *E. lucida* (entire) and *E. milliganii* ssp. *milliganii* (entire) macrofossils from Regatta Point and the Regency Formation. Although their full ecological significance

Fig. 5.15. Stratigraphic distribution of selected leaf macrofossil *Eucryphia* spp. in south-eastern Australia. The line to the left of each species represents the stratigraphic age range of the deposit in which it occurs. The likely ancestral form of *Eucryphia* (compound leaves; serrate leaflet margins; no peltiform extensions) is illustrated. The form of the ancestor is supported by the cladogram illustrated by Bradford and Barnes (manuscript submitted, Appendix 1). The scale bar for the ancestral leaf = 10 cm.

The oldest species, *E. falcata* and *E. aberensis*, had compound leaves with serrate margins. Leaves of *E. leaensis* were probably compound while those of *E. mucronata* were probably simple. The simple leaves of *E. milliganii* ssp. *milliganii* and *E. lucida* are illustrated from Regatta Point (Early Pleistocene) and are also indicative of those from the Regency Formation (Middle Pleistocene).

Peltiform extension development on the abaxial lamina and midrib is shown (far right). These structures were present by the Late Paleocene, and were well developed by the Middle to Late Eocene (*E. aberensis*), but possibly earlier as there is a gap in the fossil record with the exclusion of *E. microstoma* (see text for explanation).


Late Pleistocene
Early Pleistocene
Pliocene
Late Miocene
Middle Miocene
Early Miocene
Late Oligocene
Early Oligocene
Late Eocene
Middle Eocene
Early Eocene
Late Paleocene
Early Paleocene
Cretaceous
Ancestor
E. milliganii ssp. milliganii
E. lucida
Simple leaves
? Simple leaves
E. mucronata
E. leaensis
E. aberensis
Little Rapid River
E. aberensis
Loch Aber
E. falcata
Compound leaves
Peltiform extensions
Well developed; present on the apical midrib
Well developed; absent from the midrib
?
Poorly developed
Absent

is unclear, Hill (1991*a*) and Taylor and Hill (1996) hypothesised that the extensions present in evergreen species may reduce transpirational water loss and/or increase frost resistance. The absence of extensions in *E. glutinosa* may be, in part, due to the species' semi-deciduous habit. There may be fossils of deciduous *Eucryphia* but they are largely unrecognisable without the peltiform extensions.

Peltiform extensions were poorly developed in the Late Paleocene (*E. falcata*) but were well developed by the Middle to Late Eocene-Early Oligocene (*E. aberensis, E. leaensis* and *E. mucronata*) at the latest (Fig. 5.15). Since most authorities consider that the Early Cainozoic was very wet (e.g. Truswell 1993; Hill 1994; Macphail *et al.* 1994; Quilty 1994) it is very doubtful that the peltiform cuticular extensions initially evolved as an adaptation to reduce water loss. In particular, the oldest fossil record is at Lake Bungarby (*E. falcata*) which is likely to have been a wet environment that did not experience periods of drought or freezing conditions, and was probably a comparable habitat to extant cool temperate rainforest (Taylor *et al.* 1990). However, based on wood anatomy, Taylor *et al.* (1990) do suggest that cooler conditions caused the slowing of growth for at least some time of the year.

Furthermore, the modern relatives of other fossil taxa that co-occurred with the extinct *Eucryphia* species are not generally associated with dry climates today (e.g. Hill 1994, 1995). The current restriction of extant species to everwet cool temperate habitats from sea level to the subalpine zone and at higher altitudes in the subtropical and warm temperate zone where water would be rarely if ever limiting also goes against their palaeogeographic occurrence in a dry climate. Therefore, based on this data it is extremely difficult to argue that these cuticular features evolved in response to dry (including seasonally dry) or cold conditions or some combination of both. However, it is plausible that once evolved the enhanced development of the peltiform extensions through the Cainozoic was, at least in part, due to increasing cold, frost, dryness, seasonality or some combination of these.

A reduction from compound to simple leaves, based on the fossil record, post-dates the evolution of peltiform cuticular extensions and an entire leaf margin (Fig. 5.15). In fact, no fossil leaf species can definitely be considered to have had simple leaves, although it is probable that *E. mucronata* represents a simple leaf, in addition to those leaves of *E. lucida* and *E. milliganii* ssp. *milliganii* from Regatta Point and the Regency Formation.

The evolution of simple leaves within the genus is polyphyletic based on the cladogram of Taylor and Hill (1996), having evolved within the South American *E. cordifolia* and

Tasmanian *E. lucida* and *E. milliganii* subspecies. If *E. mucronata* is a simple leaf, then it has strong affinities to *E. cordifolia*, and may indicate that simple leaves had evolved by the Early Cainozoic in a lineage that gave rise to *E. cordifolia*. Simple leaves then independently evolved more recently in the Tasmanian species from an ancestor with compound leaves similar to *E. moorei*. This is supported by the cladogram of Taylor and Hill (1996), and the fact that leaflet reduction is not absolute in *E. lucida* and the subspecies of *E. milliganii* as some trifoliate leaves still occur (R. W. Barnes pers. obs.). A revision of the phylogenetic analysis of Taylor and Hill (1996) combined with molecular and new fossil data may further elucidate the evolution of leaf form in the genus.

Chapter 6. Miscellaneous Cunoniaceae Macrofossils

There are numerous records of Cunoniaceae fossil leaves and leaf fragments, wood and reproductive structures in the literature. These identifications are generally of lesser known or infrequently documented genera within the macrofossil record and are often difficult to verify as the original material has often been misplaced or is very difficult to obtain. This problem of verification is compounded by the fact that so little information is provided in many of the older records, which is particularly so for the fossil wood records. This chapter is arranged by genus, with the fossil record of each, if present, discussed in detail. The final section of the chapter discusses the status of those indeterminate macrofossils that have previously been suggested to have their affinities with the Cunoniaceae.

6.1 *Acsmithia* and *Spiraeanthemum*

The sister taxa *Acsmithia* and *Spiraeanthemum* were formally recognised by Hoogland (1979) but their existence as two distinct entities was initially commented upon by Smith (1952) when reviewing the Fijian and Samoan Cunoniaceae. The leaves of both genera are simple but differ in their phyllotaxy; being whorled in *Acsmithia* (Fig. 1.2.f) and opposite decussate in *Spiraeanthemum.* Leaves are generally serrate (Fig. 6.1.a) although some *Acsmithia* species may have leaves with an entire margin (e.g. Fig. 6.1.b-c). Pocket or pit domatia sporadically occur between the midrib and secondary veins over the length of the leaf (Fig. 6.1.a), and are often associated with unicellular trichomes (Hyland and Whiffin 1993). Flowers of *Acsmithia* are hermaphrodite (Fig. 1.3.b) and those of *Spiraeanthemum* are unisexual dioecious (Hoogland 1979) and are particularly small in both genera (<4 mm in diameter).

Geographically, the two genera overlap in Fiji, with *Acsmithia* extending westward into New Caledonia, the Moluccas, Papua New Guinea and north-eastern Australia while species of *Spireaenthemum* occur in Samoa, the Solomon Islands, and New Hebrides (Hoogland 1979). Plants occur in a variety of habitats but are generally most frequent in wet forest and rainforest (Hoogland 1979, 1988; Hyland and Whiffin 1993).

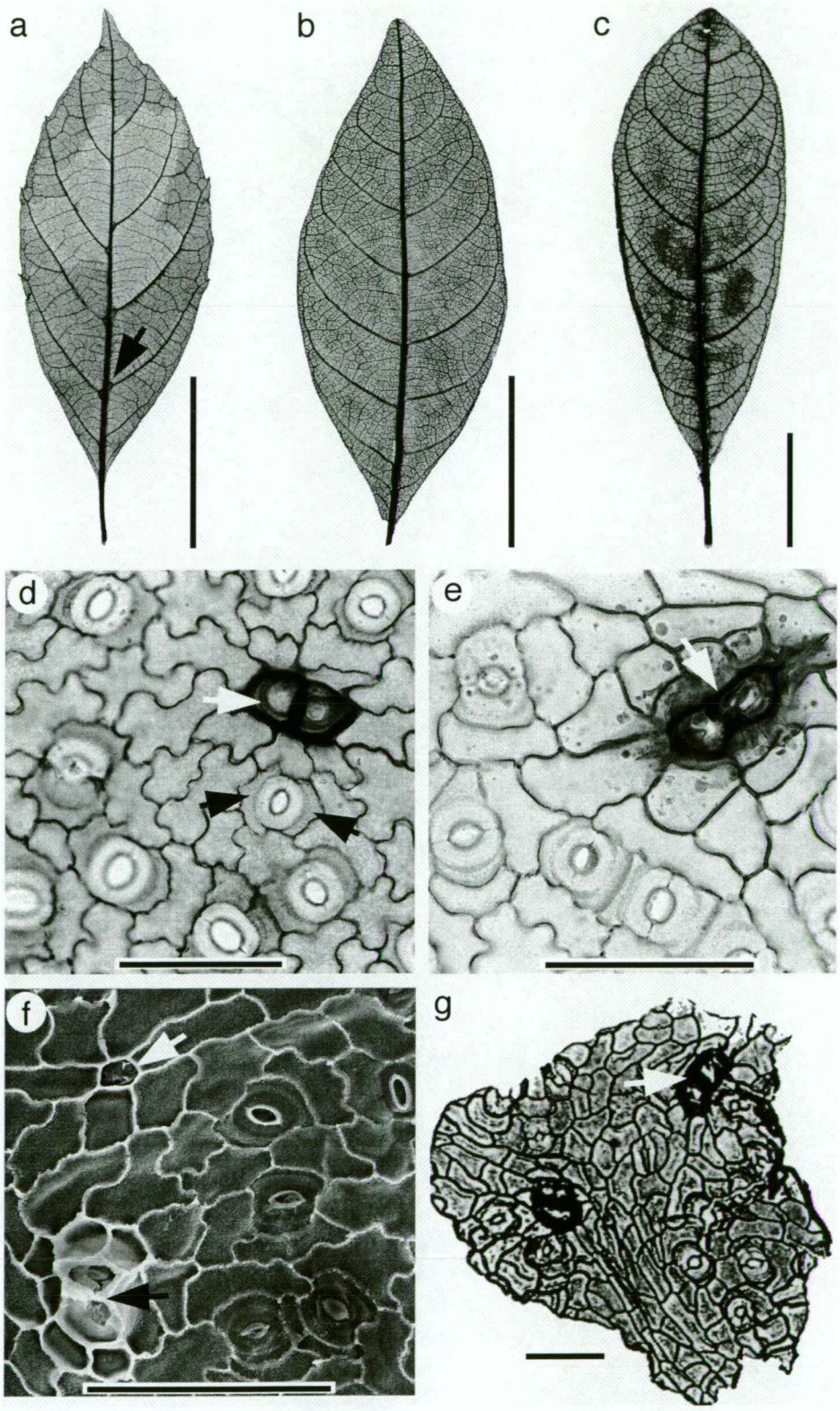
Fig. 6.1.a-f. Leaf and cuticle morphology of extant *Acsmithia* and *Spireaenthemum* species.

Figs 6.1.a-c. Leaves of extant *Acsmithia* species. The scale bar in each figure = 30 mm.
Fig. 6.1.a. *A. davidsonii* from north-eastern Queensland. Note the presence of serrations the length of the leaf. Pocket domatia are present between the midrib and secondary veins (arrow).
Fig. 6.1.b. *A. parvifolia.*
Fig. 6.1.c. *A. meridonalis.*

Figs 6.1.d-e. Light micrographs of the abaxial cuticle. Scale bar for both = 50 μm.
Fig. 6.1.d. *Acsmithia integrifolia.* Note the brachyparacytic subsidiary cell arrangement (black arrows indicate the position of each subsidiary cell) and the two cell gland (white arrow). Epidermal cells walls are slightly sinuous.
Fig. 6.1.e. *Spireaenthemum macgillivrayi.* Stoma have a brachyparacytic subsidiary cell arrangement. A two cell gland is present (arrow), mainly on the veins. Epidermal cell walls are straight to slightly sinuous.

Fig. 6.1.f. Scanning electron micrograph of the inner abaxial cuticle of *A. davidsonii.* Simple hair bases are surrounded by weakly modified epidermal cells (white arrow). Note the two cell gland (black arrow) and the position of the subsidiary cells relative to the guard cells (brachyparacytic arrangement). Scale bar = 100 μm.

Fig. 6.1.g. Light micrograph of a fragment of dispersed cuticle assigned to *Spiraeanthemum/Acsmithia* (OR1-012) from the Ooldea Range 6 core (Pidinga Formation) in South Australia. Note the presence of stoma with a brachyparacytic subsidiary cell arrangement. A two cell gland occurs on the veins (arrow). Scale bar = 50 μm.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All extant *Acsmithia* and *Spireaenthemum* species possess stoma with a brachyparacytic subsidiary cell arrangement and have two cell glandular structures on the midrib and major and minor veins (Figs 6.1.d-f). These structures are not trichomes or trichome bases as suggested by Dickison (1975*b*), rather they are secretory glands. The purpose of these glands and associated exudate remains unknown although they are particularly active in developing leaves. Trichomes are present but rare (Fig. 6.1.f), with bases formed by the slight radial modification of the cells surrounding the unicellular trichome (Fig. 6.1.f) and a foot cell is absent. The glands in these two genera are unique within the Cunoniaceae and are therefore considered to be an excellent character on which to base a formal identification, particularly when combined with leaf form, venation pattern and subsidiary cell arrangement. However, both genera, or individual species within a genus, cannot be distinguished on cuticle characters alone (see also Carpenter and Pole 1995).

Dispersed cuticle from the late Middle Eocene (Clarke 1993) Lefroy palaeodrainage (Pidinga Formation) of West Australia has been described as *Spiraeanthemum/Acsmithia* by Carpenter and Pole (1995). The cuticle preserves two cell glandular structures in association with stoma that have a brachyparacytic subsidiary cell arrangement. No whole leaves or leaf fragments were extracted. The presence of these glands and the arrangement of the subsidiary cells is clearly the same as for extant taxa and therefore the identification by Carpenter and Pole (1995) is supported. Illustrations of the fossil cuticle are provided by Carpenter and Pole (1995) and are not repeated here.

Dispersed cuticle with proposed affinities to *Spiraeanthemum/Acsmithia* (A. Rowett pers. com.) has also been extracted from the Ooldea Range 6 core that samples the Pidinga Formation in South Australia, but has not been illustrated until now (Fig. 6.1.g). The cuticle fragments preserve stomata with a brachyparacytic subsidiary cell arrangement and two celled glandular structures on the veins, homologous to those present in the extant species of both genera (Fig. 6.1.g cf. Figs 6.1.d-e). On this basis, the cuticle is here assigned to *Spiraeanthemum/Acsmithia.* Until leaves or leaf fragments have been extracted from the core it is not possible to further refine the affinities of the cuticle.

In both cases, the dispersed cuticle indicates that either one or both genera were present in the areas of deposition. However, based on the extant distribution of both genera it is more likely that the cuticle represents *Acsmithia* than *Spiraeanthemum* as the latter genus now occurs east of Fiji (see above). These fossil cuticles are

essentially derived from the same Formation (Pidinga), are of similar age (ca. Middle Eocene) and indicate a different or more widespread distribution of at least one genus during the Early Cainozoic. The genera are presently distributed in tropical and sub-tropical forests of north-eastern Australia and the South Pacific (see above; Hoogland 1979). Based on the macroflora assemblage preserved in both the Lefroy and Cowan sediments (Carpenter and Pole 1995) it is apparent that the vegetation and climate was probably comparable to that occupied by the extant species of both genera today.

Carpenter and Buchanan (1993) described a flower from Early Oligocene sediments at Cethana as the fossil taxon *Acsmithia grandiflora* on the combined presence of a superior, apocarpous gynoecium formed by multiple (4-5) carpels, actinomorphic symmetry and the absence of petals. The identification is considered valid in this study on the arguments and data provided by Carpenter and Buchanan (1993). However, the suggestion by Carpenter and Buchanan (1993) that the fossil represents a panicle is not justified as only two flowers are preserved. The inflorescence form must be considered unknown until additional, more complete, specimens are located. Leaves or leaf fragments of *Acsmithia* and/or *Spiraeanthemum* have not yet been described from the Cethana sediments.

6.2 *Anodopetalum*

A single fossil leaf has been assigned to extant *Anodopetalum biglandulosum* by Jordan *et al.* (1991) from Late Pleistocene sediments at Melaleuca Inlet in south-western Tasmania. Jordan *et al.* (1991) note that the shape of the epidermal cells, especially on the abaxial surface, is relatively consistent with those of extant specimens growing at higher altitude, which is also supported by Barnes and Rozefelds (2000; Appendix 1). This is the only fossil record of the genus.

6.3 *Bauera*

Fossil leaves and leaf fragments of extant *Bauera rubioides* have been identified by Jordan *et al.* (1991) from Melaleuca Inlet in south-western Tasmania (Fig. 6.2.a). These vegetative remains cannot be identified as either representing leaves or the lateral stipules that occur in the genus as the size and shape of both in the extant species overlap extensively (Fig. 6.2.b-c). The cuticle of fossil and extant *B. rubioides* are illustrated by Jordan *et al.* (1991) and Jordan (1992) so are not presented here. Fossil

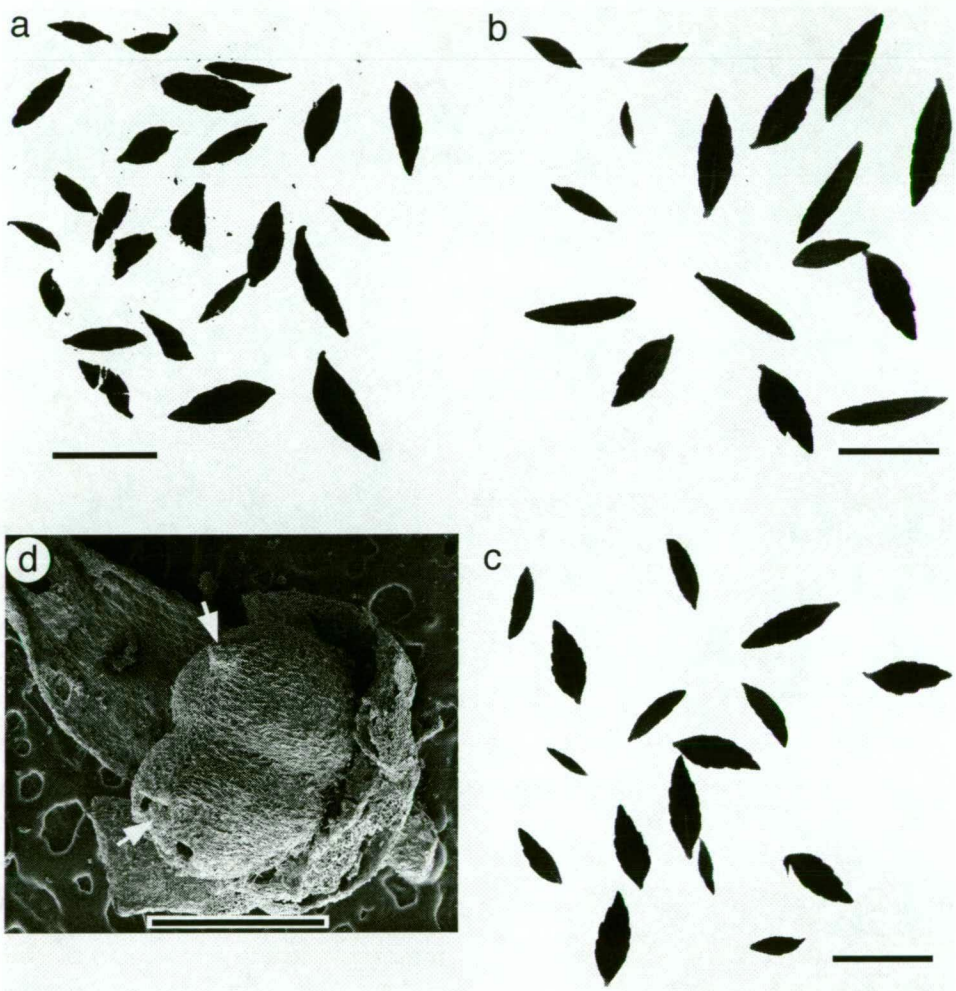
Fig. 6.2.a. *Bauera rubioides* leaf macrofossils from Melaleuca Inlet, south-western Tasmania. Scale bar = 10 mm.

Figs 6.2.b and c. Extant vegetative parts of *Bauera rubioides*. Note that the variability in size and shape overlaps between the leaves and lateral stipules. Scale bar for both = 10 mm.

Fig. 6.2.b. Leaves.

Fig. 6.2.c. Stipules.

6.2.d. Fossil capsule of *Bauera rubioides* from Melaleuca Inlet, south-western Tasmania showing bicarpellate ovary with prominent styles that are not fused (arrows indicate the position of styles, which have not been preserved in their entirety). A single sepal remains intact. Scale bar = 1 mm.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leaves of *Bauera rubioides* have also been recovered from Holocene sediments in a peat bog on Moxon Saddle in western Tasmania (Warren 1994).

A single immature capsule that is assignable to extant *Bauera* was extracted from the Melaleuca Inlet sediments by G. J. Jordan but not illustrated until now (Fig. 6.2.d). The immature fruit has a bicarpellate superior ovary that is densely pubescent. The bases of the six sepals are preserved, with one almost preserved in its entirety. The densely pubescent globose carpels with slightly offset and unfused styles, combined with the radiating six sepals is diagnostic of *Bauera* within the Cunoniaceae. The capsule probably represents extant *B. rubioides* as it co-occurs with the vegetative remains of this species (Fig. 6.2.a).

6.4 *Caldcluvia* and *Caldcluvioxylon*

Czajkowski and Rosler (1986) described an Early Tertiary macroflora from the South Shetland Islands, near Ardley Island adjacent to the Antarctic Peninsula. Macrofossils included lobed or incomplete leaf impressions of *Caldcluvia mirabilis* and *?C. mirabilis* (see Czajkowski and Rosler 1986). This identification was based on the similarity of the specimens to those described by Dusén (1908) as representing a stipule which he named *Caldcluvia mirabilis*. The secondary venation pattern is brochidodromous where there are lobes, and semicraspedodromous or craspedodromous where serrations are present. Extant *Caldcluvia paniculata* leaves are simple and regularly serrate (see Fig. 1.2.g) with straight secondary veins that terminate at a glandular sinus. The leaves are never lobed, even in juvenile foliage, and brochidodromous venation is always absent. Li (1994) redescribed these specimens as *Lomatia mirabilis* and indicated that they had a leaf morphology quite unlike that of extant *C. paniculata*. I agree that these fossil specimens have no affinities to extant *Caldcluvia* or any Cunoniaceae genus.

Petrified wood from near the Collins Glacier on King George Island was compared to that described as *Caldcluvioxylon propaniculata* by T. Torres (Prof. Lemoigne pers. com. to Shanzhen and Qingzhi (1994)). However, Shanzhen and Qingzhi (1994) indicate that the type of pitting in the fossil wood from the Collins Glacier is rounded to transitional, which is quite distinct from the scalariform pitting in extant *Caldcluvia* (Rancusi *et al.* 1987), and they even use this difference to erect a new fossil taxon, *C. collinsense*. As the pitting in the fossil and extant taxa differs, the identification of the fossil wood as having affinities to extant *Caldcluvia* is rejected in this study unless

further support is provided by more definitive characters, or a combination of characters.

6.5 *Cunonia*

The fossil species, *Cunonia europea*, described by Unger (1866) from Radoboj in Croatia (Fig. 6.3.a) is most likely incorrect based on the modern distribution of the genus alone (i.e. South Africa and New Caledonia, Hoogland *et al.* 1997). Unger (1866) compared the leaf form and venation of the fossil to modern *Cunonia capensis* (Fig. 6.3.b), which is the only South African species of the genus (Palmer and Pitman 1972). The fossil species has been described elsewhere as *Platanus* (see Mai 1995) and thus there is no fossil record for *Cunonia.*

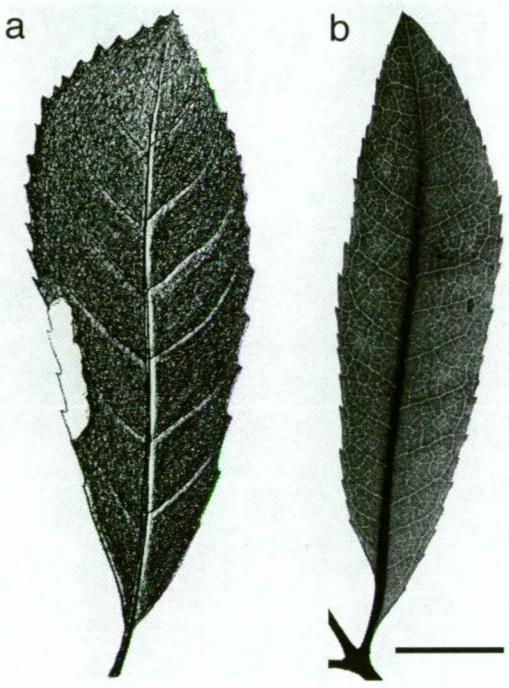
6.6 *Geissois*

The cuticle assigned to aff. *Geissois* sp. by Blackburn (1985) is described as having stomata arranged in areoles with an anomocytic or anisocytic subsidiary cell arrangement and large hydathodes on the veins. The presence of hydathodes on the veins is a relatively common feature in Cunoniaceae (see also Dickison 1975*b*), in addition to the occurrence of stomata in areoles, so these characters are of no use in assigning affinities within the genus. The presence of an anomocytic subsidiary cell arrangement in *Geissois* was not supported by the examination of specimens in this study, rather all species have a brachyparacytic subsidiary cell arrangement. Therefore, any possible affinities of this dispersed cuticle to extant *Geissois* are discounted on this character alone. The fossil cuticle may represent a species of another Cunoniaceae genus, such as *Weinmannia*, which is often variable for subsidiary cell arrangement (see Bradford and Barnes manuscript submitted, Appendix 1), although in general the cuticle lacks any diagnostic features to convincingly assign it to any extant taxon with confidence.

The wood described as *Praegeissois weindorferi* by Scott (ca. 1937) from Barrington (?Miocene) in Tasmania was not examined during this study. The wood was considered by Scott (ca. 1937) to be most similar to, but distinct from, extant Australian *Geissois* so he assigned it to a new genus *Praegeissois*. The identification by Scott (ca. 1937) may be invalid but cannot be fully assessed in the absence of the original specimen or a more detailed description of the fossil wood anatomy.

Fig. 6.3.a. Line drawing of fossil *Cunonia europea*. Unger (1866) described this species from Miocene sediments at Radoboj, Croatia. The drawing is taken from Unger (1866) as the original specimen could not be located. The drawing illustrates a craspedodromous secondary venation pattern and falcate leaf base(arrow). Unger (1866) compared the fossil to *Cunonia capensis* from South Africa (see below) and also to *Caldcluvia paniculata* from Chile.

Fig. 6.3.b. Lateral leaflet of extant *Cunonia capensis* from South Africa. Note the prominent falcate leaf base where it attaches to the rachis. Scale bar = 20 mm.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Therefore, it will be excluded from this study until a more detailed examination of the original material can be made.

6.7 *Phyllites yallournensis*

The fossil taxon *Phyllites yallournensis* is a common macrofossil in the Oligo-Miocene Morwell and Yallourn Formations in Victoria (see Blackburn and Sluiter 1994). The taxon was initially compared to leaves of some Banksineae (Proteaceae) by Cookson and Duigan (1950) on whole leaf morphology but they discounted any affinity to Proteaceae on the basis of cuticular characters. Blackburn (1985) later considered the taxon to have affinities with Cunoniaceae on leaf and epidermal morphology.

The leaves of *P. yallournensis* are pinnately lobed with brochidodromous secondary venation (Cookson and Duigan 1950; Blackburn and Sluiter 1994) and have stomata with a more or less anomocytic subsidiary cell arrangement (Blackburn 1985), although some appear to be of the anisocytic or encyclocytic type in the illustrations provided by Cookson and Duigan (1950). No extant genera of Cunoniaceae have a leaf form approaching that of *P. yallournensis* (see also Dickison 1975*b*), particularly those with an anomocytic subsidiary cell arrangement (e.g. *Callicoma*). Therefore, *P. yallournensis* is considered here to have no closer affinities to the family Cunoniaceae than to some other families, such as Rosaceae, and is excluded from any further discussion.

Blackburn and Sluiter (1994) suggest that the association of *P. yallournensis* leaves and tricolporate pollen in the same coal seam indicates that they may be derived from the same plant. As *P. yallournensis* does not represent Cunoniaceae it is unlikely that this tricolporate pollen, assigned to Cunoniaceae by Blackburn and Sluiter (1994), was derived from the same taxon.

6.8 *Schizomeria*

A single fossil flower from Cethana has been described by Carpenter and Buchanan (1993) as *Schizomeria tasmaniensis*. The specimen is an actinomorphic flower, with a prominent disk surrounded by a 5 lobed calyx. Small apically furcate petals are present, which occur in the extant Cunoniaceae genera *Platylophus, Schizomeria,*

Anodopetalum and *Ceratopetalum*. The thickened margin of the disc, as described by Carpenter and Buchanan (1993), may be the remnants of an annular nectary, present in extant species of *Schizomeria* (J. C. Bradford pers. com.).

The fossil flower conforms to the floral structure present in extant *Schizomeria* species and was distinguished by Carpenter and Buchanan (1993) from those flowers of other extant genera with furcate petals on the basis of petal shape, size and the extent of apical furcations. Petals are only weakly furcate in *Anodopetalum* (Barnes and Rozefelds 2000, Appendix 1), while long furcations occur in the petals of the single petalous *Ceratopetalum* species (*C. gummiferum*, Chapter 3 this study) and the petals of *Platylophus* are nearly as large as the sepals, which is not the case in the fossil specimen. On this basis, I agree with the identification by Carpenter and Buchanan (1993).

6.9 *Vesselowskya*

A leaf macrofossil from Cethana (Early Oligocene) was assigned to *Vesselowskya* aff. *rubifolia* by Carpenter and Buchanan (1993) on the basis of leaf form, secondary and tertiary venation patterns, subsidiary cell arrangement and the form of the trichome base. However, Carpenter and Buchanan (1993) interpret the subsidiary cell arrangement of the fossil specimen to be anomocytic. After examining the extant cuticle of *Vesselowskya* by scanning electron microscopy I consider the taxon to have encyclocytic stomata, with a ring of small cells surrounding the guard cells. I also interpret the fossil cuticle to possess encyclocytic stomates so this re-interpretation does not alter the initial interpretation of Carpenter and Buchanan (1993) that the fossil represents *Vesselowskya*.

The fossil is distinguished by Carpenter and Buchanan (1993) from the extant taxon by the basally convex shape of the serrations, which is distinct from the straight, acuminate or concave shape present in leaves of the extant species. After the examination of numerous living and herbarium specimens, I agree that basally convex teeth appear to be absent from the extant species. However, despite this difference in tooth architecture there is no doubt that there is a strong relationship between the fossil and extant species.

6.10 *Weinmannia, Weinmanniaphyllum* and *Weinmannioxylon*

6.10.1 Extant Morphology

Weinmannia is a frequent tree or small shrub in cloud or upland montane forests throughout South and Central America, Madagascar, South East Asia, Papua New Guinea, the South Pacific Islands and New Zealand (Fig. 1.1; Hopkins 1998*a*) but it is absent from Africa and Australia. The genus has opposite decussately arranged leaves with interpetiolar stipules (Fig. 6.4.b-c; Bradford 1998; Hopkins 1998*a, b, c*; Hopkins and Florence 1998). Leaves are unifoliolate (?simple) (Fig. 6.4.b and d), trifoliate or more frequently imparipinnate (Fig. 6.4.c and e), with significant variation among and within species for the number of leaflets. Many species with imparipinnate leaves have a prominently winged rachis between the leaflets (e.g. Fig. 6.4.c and e; e.g. Bernardi 1963*b*; Hopkins 1998*a*), which is particularly common and well developed in the species of the Americas.

Secondary venation in most leaves or leaflets is of the craspedodromous type, with the secondary veins terminating at the leaf margin. However, these veins do not terminate at a tooth apex (Fig. 6.4.d) but instead terminate at a glandular, often pubescent, sinus where another vein originates to vascularise the tooth apex. This craspedodromous venation pattern is in contrast to some other Cunoniaceae genera, for example in *Callicoma* the secondary venation is also craspedodromous but the secondary veins terminate at a tooth apex, with tertiary veins vascularising the sinus (see Fig. 4.3.c-e, Chapter 4 this study). Semicraspedodromous venation also occurs in some leaflets and leaves, and is often expressed in leaves on the same plant that also has leaves with craspedodromous venation. In the semicraspedodromous type, the secondary vein bifurcates just within the leaf margin, with one vein vascularising the sinus as described above and the other looping to anastomose with the proximal secondary vein, as also described by Hopkins (1998*a*).

The leaf cuticle of *Weinmannia* has not been described or illustrated prior to this study. As the genus contains numerous and widespread species (c.150 spp., Hopkins 1998*a*), not all were examined during this study. After examining 39 species it was found that little variation exists within or across species in what are regarded to be taxonomically important characters, such as trichome bases.

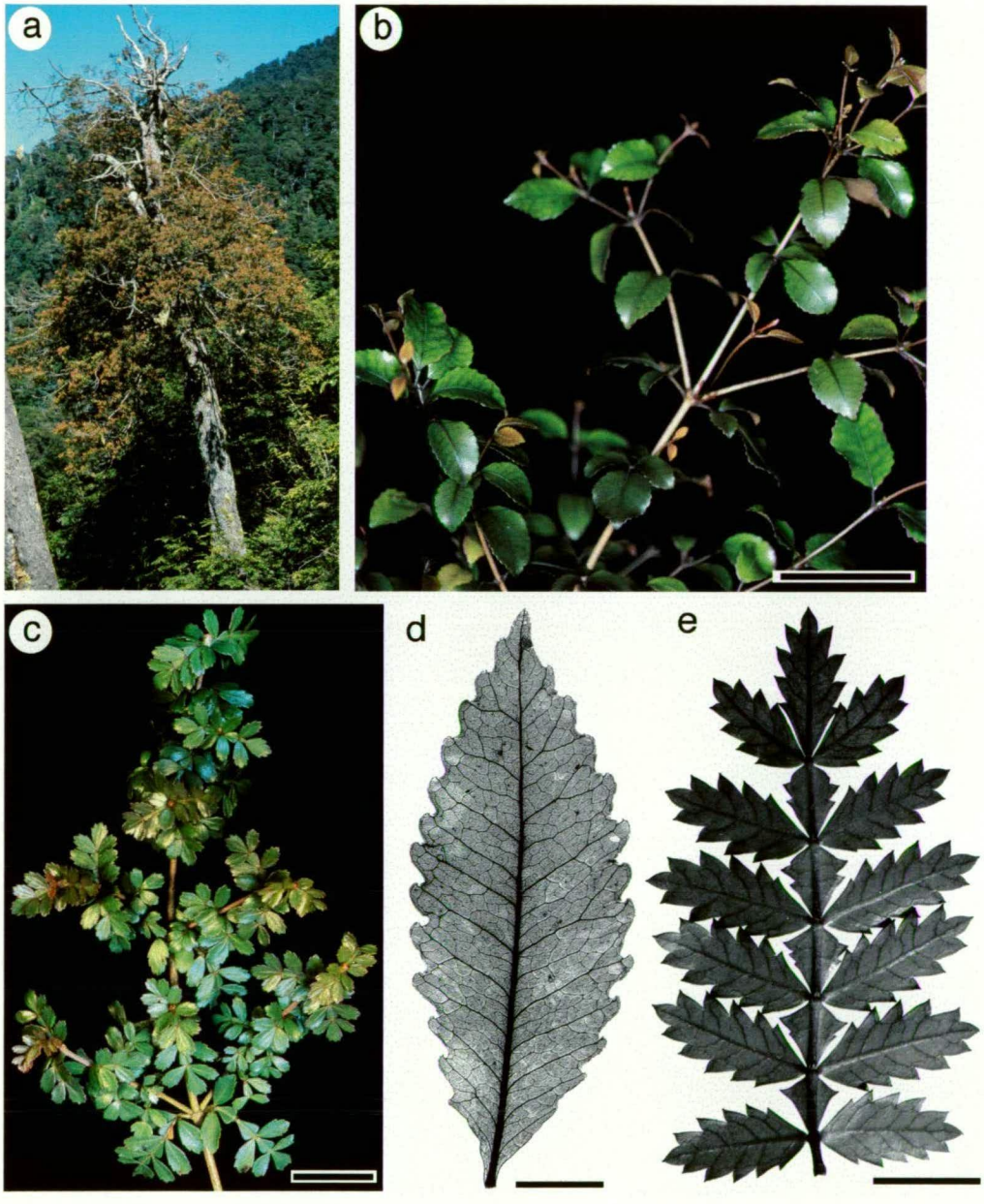
Fig. 6.4.a. *Weinmannia trichosperma* growing in its native forest habitat in Chile, South America. It is usually a canopy tree, often emerging from a dense understorey of bamboo (*Chusquea* sp.), and takes on a bright red appearance when the seed capsules are nearly mature. The tree illustrated is approximately 15 m tall.

Fig. 6.4.b. *Weinmannia racemosa* from New Zealand showing opposite decussate leaves. Leaf form is predominantly unifoliate although tri- or bifoliate leaves are also present, but uncommon. Scale bar = 10 cm.

Fig. 6.4.c. *Weinmannia* sp. from Ecuador showing opposite decussate imparipinnate leaves. Leaves are formed by 5-9 leaflets with a prominent winged rachis between each successive leaflet, which is a common feature in South and Central American species and also occurs in species from Madagascar and the South Pacific Islands. Scale bar = 35 mm.

Fig. 6.4.d. Cleared unifoliate leaf of *W. racemosa* showing a craspedodromous secondary venation pattern. Secondary veins terminate at a glandular sinus at the leaf margin, from where a tertiary vein then vascularises the glandular tooth apex. Scale bar = 10 mm.

Fig. 6.4.e. Imparipinnate leaf of *W. trichosperma* showing a mixed craspedodromous and semicraspedodromous secondary venation pattern. Secondary veins usually terminate at a glandular sinus at the leaf margin (craspedodromous type), or rarely bifurcate near the sinus where one branch terminates at the sinus and the other loops to the weakly anastomose with the proximal secondary vein (semicraspedodromous type). Note the winged rachis between successive leaflets. Scale bar = 10 mm.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The abaxial surface is usually smooth and non-ornamented with superficial stomata (Fig. 6.5.a-b). Epidermal cell shape and size is variable, ranging in shape from isodiametric, square, to rhomboidal (e.g. Fig. 6.5.c-e). Occasional unicellular trichomes are present on the midrib, veins (Fig. 6.5.c) and rarely within the areoles (e.g. *W. pubescens*) and have bases formed by 5-8 radially modified epidermal cells (Fig. 6.5.c). There is slight thickening around the base of the trichome. In addition to these trichomes, and unique to *Weinmannia*, is another form of trichome with a base formed by numerous small epidermal cells (Fig. 6.5.d, f-g). Hopkins (1998*a*) termed these structures as '...black dots, which are probably the bases of caducous hairs...'. These 'complex' trichomes do not occur in all species, but are not restricted in their distribution to a specific section of *Weinmannia*, leaf form or group of species within a certain geographic region. This trichome type occurs on both the abaxial and adaxial leaf surface in those species in which they occur (e.g. Fig. 6.5.d, f). The multicellular structures that occur on the leaves of some *Elaeocarpus* and *Sloanea* species are glands and can be distinguished from those structures in *Weinmannia* by the lack of an emergent trichome (see figures in Turnbull 1986). A prominent hole is present in those multicellular bases where the trichome has been shed (Fig. 6.5.f-g) so that they can be identified even without the emergent trichome.

These multicellular trichome bases are also present in X-it (Fig. 6.5.h), which is a single plant from New Zealand that was assigned to Cunoniaceae on combined leaf and stem morphology and sequences of the chloroplast *rbc*L gene (see Garnock-Jones *et al.* 1996). The presence of these trichomes in this plant further supports a link to Cunoniaceae, and in particular, to *Weinmannia*. Garnock-Jones *et al.* (1996) even suggest that the plant may represent a dwarf mutant form of *W. racemosa* which is abundant in the wet forests of New Zealand (Hopkins 1998*c*), and is a hypothesis supported by this cuticular study (i.e. Fig. 6.5.h cf. Fig. 6.5.d).

As indicated by Carpenter and Buchanan (1993) and Hoogland *et al.* (1997), some species of *Cunonia* also possess imparipinnate leaves with a winged rachis between successive leaflets (e.g. *C. pterophylla*, Fig. 6.6.a). The venation pattern in both *Cunonia* and *Weinmannia* imparipinnate leaves with a winged rachis is indistinguishable, being of the craspedodromous or semicraspedodromous type described previously. The subsidiary cell arrangement in *Cunonia* is anisocytic (e.g. *C. capensis*, Fig. 6.6.b), which also occurs in all *Pancheria* species (*P. engleriana*, Fig. 6.6.c) and in some *Weinmannia* species (e.g. *W. humblotii*, Fig. 6.6.d). *Cunonia* and *Pancheria* do not have the multicellular trichome bases present in some *Weinmannia* species so the genera are distinguishable on this character alone if they are

Fig. 6.5.a-g. Scanning electron and light micrographs of cuticular features of selected extant *Weinmannia* species.

Fig. 6.5.a. Outer abaxial cuticle of *W. richii*. Note the superficial stomata and the lack of any surface ornamentation. Scale bar = 250 μm.

Fig. 6.5.b. Outer abaxial cuticle of *W. bojeriana* showing superficial stomata and no surface ornamentation. Scale bar = 150 μm.

Fig. 6.5.c. Light micrograph of the abaxial cuticle of *W. serrata*. Unicellular trichomes occur on the veins (arrows). Subsidiary cell arrangement in this species is of the anisocytic type. Scale bar = 100 μm.

Fig. 6.5.d. Light micrograph of a multicellular trichome base on the abaxial cuticle of *W. racemosa*. The base is formed by numerous small epidermal cells, with an emergent single unicellular trichome (arrow). Scale bar 50 μm.

Fig. 6.5.e. Inner abaxial cuticle of *W. sylvicola* showing a single stoma. Note the encyclocytic arrangement of subsidiary cells around the guard cells (positions indicated by arrows). The subsidiary cells are small and radially arranged around the guard cells. Scale bar = 45 μm.

Fig. 6.5.f. Outer adaxial surface of *W. bojeriana* showing a multicellular trichome base (arrow). The cuticle is smooth and non-ornamented. Scale bar = 100 μm.

Fig. 6.5.g. Higher magnification of figure 6.5.f showing the multicellular trichome base. The arrow indicates the insertion point of the trichome. Scale bar 50 μm.

Fig. 6.5.h. Light micrograph of the abaxial cuticle of X-it from New Zealand showing a multicellular trichome base. Note the central trichome (arrow). Scale bar = 50 μm.

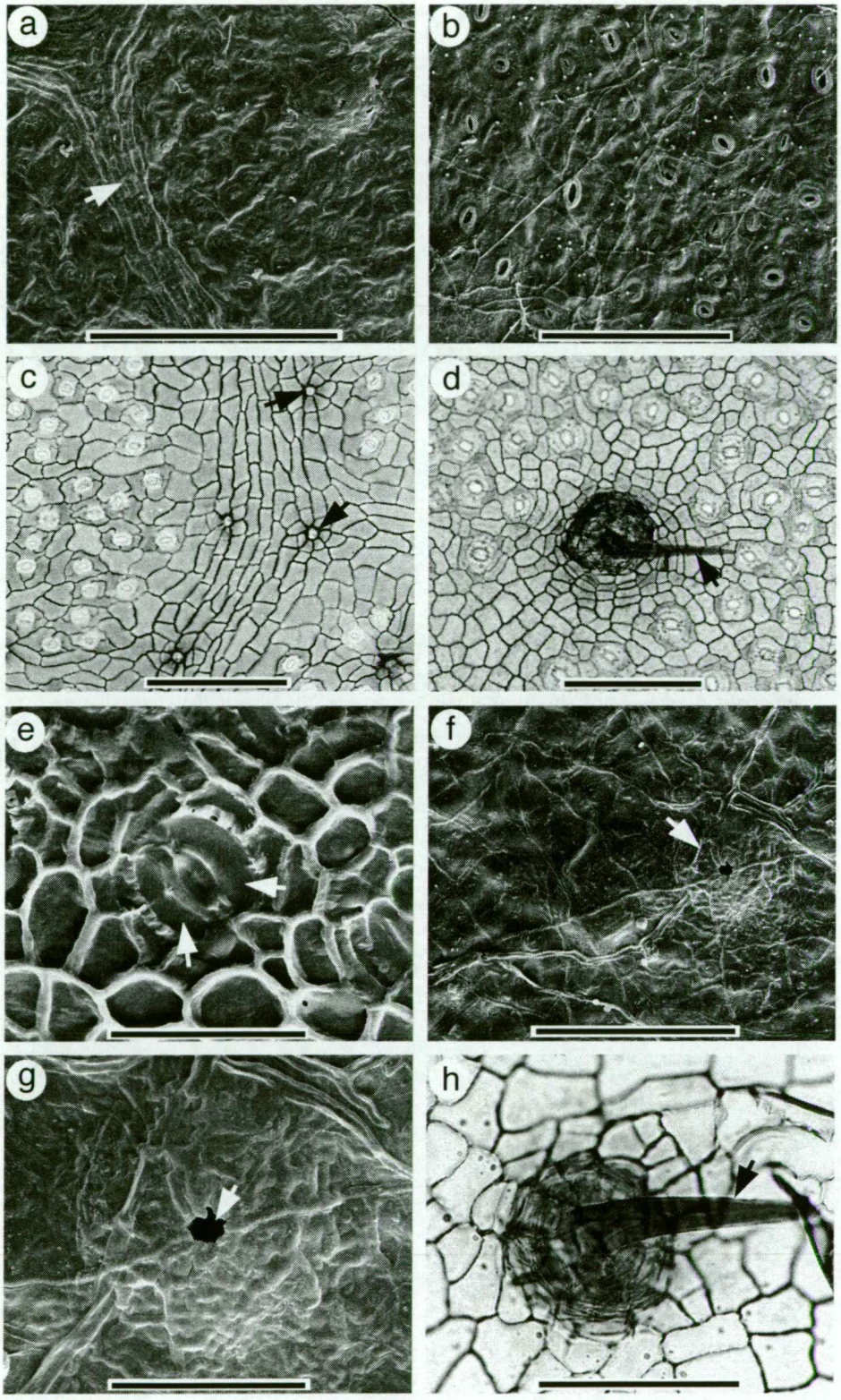
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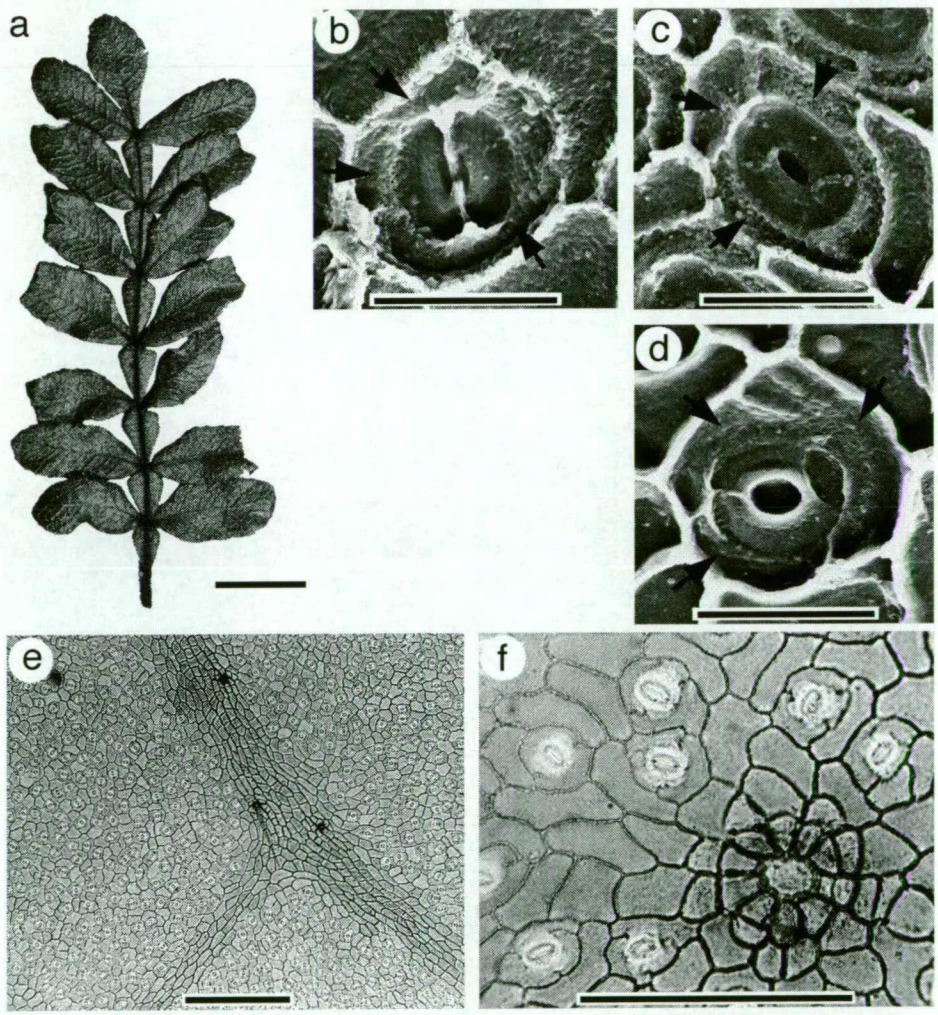
Fig. 6.6.a. Imparipinnate leaf of *Cunonia pterophylla* from New Caledonia. The lateral leaflets are serrate and the rachis between the leaflets is winged. Scale bar = 20 mm.

Figs 6.6.b-d. Scanning electron micrographs of the inner cuticle showing the anisocytic subsidiary cell arrangement in a single species each for the genera *Cunonia, Pancheria* and *Weinmannia.* The position of each subsidiary cell is indicated by an arrow in each figure. Scale bar in each figure = 25 μm.
Fig. 6.6.b. *Cunonia capensis.*
Fig. 6.6.c. *Pancheria engleriana.*
Fig. 6.6.d. *Weinmannia humblotii.*

Figs 6.6.e-f. Light micrographs of the abaxial cuticle of selected extant *Cunonia* species.
Fig. 6.6.e. *C. linearisepala.* Note the lack of multicellular trichome bases. Unicellular trichomes are present on the major veins (small black dots in figure). Scale bar = 200 μm.
Fig. 6.6.f. *C. lenormandii.* Note the anisocytic subsidiary cell arrangement and the presence of a unicellular trichome base (lower right) formed by 10 radially arranged epidermal cells. Scale bar = 100 μm.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present, irrespective of leaf form. The abaxial surface of *Cunonia* is generally smooth and non-ornamented with sparse unicellular trichome bases occurring on the major and minor veins (Fig. 6.6.e). Trichome bases are formed by numerous (6-12) radially modified epidermal cells (Fig. 6.6.f).

Some leaf morphological features of *Cunonia* and *Weinmannia* are listed in Table 6.1. The single feature that can be used to distinguish imparipinnate leaves of *Weinmannia* from those of *Cunonia* is the presence of multicellular trichome bases. However, in the absence of these structures, identification becomes difficult and may not be possible to the generic level. Any affinities to *Cunonia* can be discounted if the subsidiary cell arrangement in the fossil leaf is anomocytic, encyclocytic or brachyparacytic, as all *Cunonia* species have anisocytic stomata (see Fig. 6.6.b).

6.10.2 Fossil Record

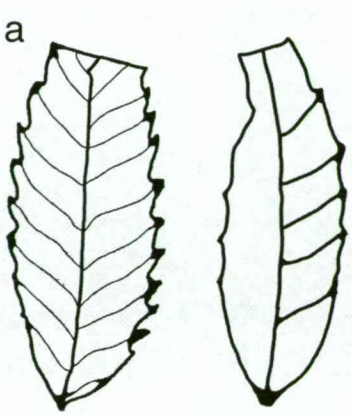
6.10.2.1 Historical Records

The genus *Weinmannia* is well documented as a micro- and macrofossil (e.g. McGlone 1983; McGlone and Bathgate 1983; Hooghiemstra 1989; Mildenhall 1994; Berry 1917; Carpenter and Buchanan 1993). Milligan (1849) recorded fossils in limestone of unknown age (?Tertiary) from Knocklofty in Hobart, Tasmania, as 'Impressions of leaves and the cast of a seed vessel like those of the *Weinmannia*' which occurred with fossil leaves or fruits of *Banksia, Sassafras, Phebalium* and *Leptospermum*. For Milligan (1849) to make such a definitive identification it is likely that the leaf specimens were imparipinnate leaves with a winged rachis between the leaflets, present in some species of *Weinmannia* and *Cunonia*. Alternatively, Milligan (1849) may have been referring to a number of species which are now in different genera of the Cunoniaceae (e.g. *Weinmannia biagiana* = *Geissois biagiana*, *Weinmannia lachnocarpa* = *Pseudoweinmannia lachnocarpa*, *Weinmannia rubifolia* = *Vesselowskya rubifolia*). In the absence of any illustrations by Milligan (1849) or any specimens this fossil leaf and reproductive record remains unverified.

Alleged *Weinmannia* leaflets have been recovered from Pliocene sediments near Potosi in eastern Bolivia and were described as the two species *W. brittoni* and *W. potosina* by Berry (1917, Fig. 6.7.a). The latter species was re-described from the taxon *Myrica potosina* (Britton 1893) as Berry (1917) considered the leaf form to be more representative of extant *W. glabra*, now common in the West Indies, South America

Fig. 6.7.a. Line drawings of *Weinmannia potosina* (Britton) ?leaflets from the Potosi deposit in Bolivia. The line drawings are those done by Britton (1893) who described the leaves as *Myrica potosina*. Berry (1939) later considered them to be more representative of the leaflets of extant *Weinmannia* species so assigned them to that genus. The original specimens could not be located.

Fig. 6.7.b. Incomplete macrofossil described as (?)*Weinmannia* sp. by Chapman (1926) from Narracan, South Gippsland in south-eastern mainland Australia. The original specimen could not be located for a direct examination during this study. Scale bar = 10 mm.


a


b

(Venezuela, Colombia and Guiana) and southern Mexico. The specimens described as *Weinmannia* may be lateral leaflets as they possess a weakly falcate leaf base (Fig. 6.7.a). In addition to these records, Berry (1917) commented that 'Upwards of a score of fossil species [*Weinmannia*] have been described, mostly from Europe and North America, and well-preserved and undoubted forms are present in the Miocene lake deposits at Florissant, Colorado'. However, the leaf macrofossils assigned to *Weinmannia* (including *W. haydenii, W. integrifolia, W. lesquereuxi, W. obtusifolia* and *W. phenacophylla*) from the Florissant Beds have been re-described by MacGinitie (1953) as representing species of the genus *Athyana* which currently occurs in Argentina, Paraguay and Bolivia. The removal of these fossil leaves from *Weinmannia* by MacGinitie (1953) is supported here, however the validity of assigning them to *Athyana* is unknown and beyond the scope of this study to investigate.

Krasser (1904) described *W. bahiana* from Pliocene sediments in the Bahia Province of Brazil. As with *W. brittoni*, the fossil taxon was suggested to have affinities with the extant species *W. glabra*, however Krasser (1904) fails to provide any illustrations or descriptions of the fossil.

Fossil *Weinmannia* species have been described from Europe (e.g. Andreanszky 1959) but these are no longer considered to represent the genus (see Mai 1995) so are not discussed in this study.

Leaf venation was used by Chapman (1926) to describe two incomplete fossil leaves from Tertiary sediments at Narracan, South Gippsland, Australia, as (?) *Weinmannia* sp. (Fig. 6.7.b). The venation patterns were compared to those present in extant *Weinmannia biagiana*, which is now *Geissois biagiana*. There are not enough data provided in the illustration and description of (?) *Weinmannia* sp. (= *Geissois* sp. due to taxonomic name change) by Chapman (1926) to assign the fossil specimen to any extant genus with any level of confidence. Even in the event of the original specimens being located, it is unlikely that they preserve enough features to warrant formal identification.

In general, the illustrations and descriptions of all of these older specimens, when provided, are very superficial and contain little or no information on the leaf venation pattern and cuticular morphology. Without any of the original specimens examined by Berry (1917) and other researchers these older leaf macrofossil records of *Weinmannia*

are unverified and will be excluded from any further discussion until a more definitive identification can be made.

6.10.2.1 Modern Records

More recently, Carpenter and Buchanan (1993) have described several leaf macrofossils from Cethana (Early Oligocene) as having affinities to extant *Weinmannia* or *Cunonia* as they represent imparipinnate leaves with a winged rachis between successive leaflets that have a serrate margin. The assignment of the macrofossils to either extant genus was not possible due to the morphological overlap between the genera in leaf form and the lack of cuticular preservation. Hence, the genus *Weinmanniaphyllum* was erected to accommodate those leaf macrofossils that have leaf architectural similarities to some extant *Weinmannia* and *Cunonia* species but cannot be assigned to either with confidence. Features of *Weinmanniaphyllum* include imparipinnate leaves with an elongated terminal leaflet, a serrate leaflet margin, a winged rachis between leaflets and semicraspedodromous venation with secondary veins terminating at a glandular sinus (see Carpenter and Buchanan 1993). The specimens examined by Carpenter and Buchanan (1993) were placed in the single taxon *Weinmanniaphyllum bernardii* with possible closer affinities to *Weinmannia* on the basis that the high number of leaflets in some macrofossils (>12 pairs) does not occur in any extant *Cunonia* species. However, Hoogland *et al.* (1997) have since described at least one extant *Cunonia* species with leaves of more than 12 lateral pairs of leaflets (*C. varijuga*).

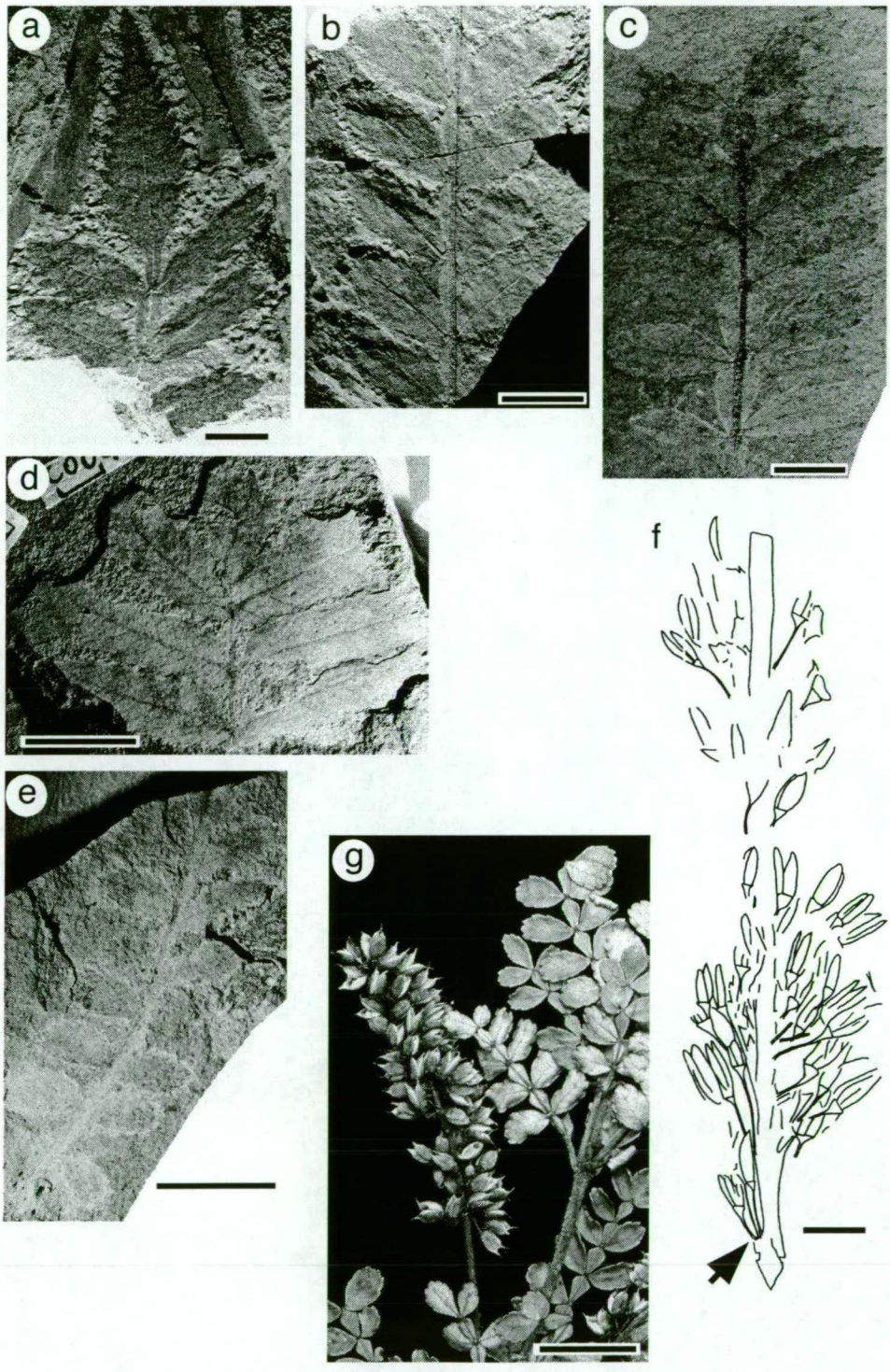
I agree with the comments of Carpenter and Buchanan (1993) for the need to erect *Weinmanniaphyllum*, however in this case, the single taxon *W. bernardii* probably encompasses at least two, perhaps three, different taxa based on the differences in leaf architecture and leaflet shape. Specimens either have; (i) long thin leaflets that leave the rachis at an angle less than 30°, and an unevenly winged rachis (Fig. 6.8.a, c-d), (ii) leaflets of almost equal length and width leaving the rachis at an angle exceeding 50°, and a very regularly winged rachis (Fig. 6.8.b) or (iii) extremely small (<5 mm), almost ovate leaflets, and only the weak development of a winged rachis (Fig. 6.8.e). However, and as commented upon by Hopkins (1998*a*), some extant *Weinmannia* species are quite variable in leaf form, particularly for leaflet number, shape and size. Marked differences between juvenile and adult foliage of a single species often exacerbates this problem (Hopkins 1998*a*). In recognition of this, the different macrofossil 'forms' are not assigned formal names here, but instead attention is drawn

Figs 6.8.a-e. *Weinmanniaphyllum bernardii* R.J. Carpenter & A.M. Buchanan from Cethana, north-central Tasmania. Scale bar for all except figure 6.8.c = 10 mm.

Fig. 6.8.a. C-377 (holotype).
Fig. 6.8.b. C-060.
Fig. 6.8.c. C-1023. Scale bar = 5 mm.
Fig. 6.8.d. C-004.
Fig. 6.8.e. C-1024.

Fig. 6.8.f. ?*Weinmannia racemosa* inflorescence from the Manuherikia Group (Early Miocene) in New Zealand. The line drawing is by Pole (1993) as the original specimen could not be obtained. Scale bar = 10 mm.

Fig. 6.8.g. Extant *W. fagaroides* from Ecuador showing dehisced capsules arranged in a terminal raceme. Leaves are compound and the rachis is prominently winged between the leaflets. Scale bar = 20 mm.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to the fact that they may represent different species. Cuticular or surface features may provide further characters on which to separate these 'forms', although to date no *Weinmannia/Cunonia* specimens from Cethana, including those collected during this study, have any organic preservation. The location of organic remains may also provide further data (i.e. subsidiary cell arrangement and the form of trichome bases) to assign the macrofossils to either *Cunonia* or *Weinmannia* and not to the form genus *Weinmanniaphyllum.*

A fossil reproductive structure (Fig. 6.8.f) from the Early Miocene Manuherikia Group in New Zealand has been assigned to ?*Weinmannia racemosa* by (Pole 1993*b*). It is easy to recognise why Pole (1993*b*) assigned affinities to *Weinmannia* given the racemose form of the infructescence (e.g. Fig. 6.8.g). Pole (1993*b*) interprets the structure to be a simple raceme, with bicarpellate capsules that occur on the end of each stalk (pedicel). I agree that the fossil probably represents a raceme composed of bicarpellate ventrally dehiscent capsules with a basal receptacle. Based on the line drawing by Pole (1993*b*, Fig. 6.8.f), it appears that the fruits (flowers) were clustered into groups, originating from a single node (see arrow in Fig. 6.8.f). This floral development and raceme form, termed fasciculate by Bradford (1998) in his revision of *Weinmannia*, occurs in sections *Weinmannia, Fasciculata, Inspersa, Spicata* and a single species of *Cunonia, C. pulchella* (see Bradford 1998). The reproductive structure does not belong in *Cunonia* as it has ventrally dehiscent capsules and is distinguished from those infructescence in other Cunoniaceae genera (e.g. *Lamanonia, Vesselowskya, Geissois, Pseudoweinmannia*) by the fasciculate development. If the infructescence is *Weinmannia* then it does not have affinities to the two extant New Zealand species (*W. racemosa and W. sylvicola*) as these have solitary floral development and are placed in the section Leiospermum by Bradford (1998). The specimen probably represents an extinct species and is here referred to as ?*Weinmannia* sp. indet. Extant species in the sections with similar floral development are distributed throughout South and Central America, Mascarenes, Madagascar, Indonesia, Papua New Guinea, the Philippines and many South Pacific Islands (Bradford 1998).

Fossil seeds extracted from sediment in Lady Lake (5,700-5,400 years B.P.) in New Zealand have been identified as *W. racemosa* by Pocknall (1980) but were not described or illustrated. The affinity of the seeds cannot be commented upon here in the absence of the original specimens or suitable information to determine the validity of the identification, although it may be valid given the widespread occurrence of *W. racemosa* in New Zealand today (e.g. Wardle 1966).

A single fossil specimen of *Weinmannia* from Wilson's Creek is that of an imparipinnate leaf formed by 12 lateral leaflets and a slightly elongated terminal leaflet (Fig. 6.9.a). The leaf is extremely small (27 mm in length) and all the intact lateral leaflets have an entire margin. Small teeth are present in the apical portion of the terminal leaflet (see arrow in Fig. 6.9.a). The rachis is prominently winged between each successive leaflet with each wing having an entire margin (Fig. 6.9.a). The venation in each leaflet is difficult to determine, although in the upper leaflets it appears to be brochidodromous, and semicraspedodromous where the veins are associated with teeth in the terminal leaflet.

The cuticle of the specimen is very fragile and consequently it was not possible to remove it from the other organic remains without destroying it. Therefore, after being treated with hydrofluoric acid the organic fragments were placed directly onto an aluminium stub for scanning electron microscopy (see '2.2.1 Cuticle Preparation'). As the cuticle was prepared in this way, only the outer surface features were viewable for this study. Stomata are poorly preserved (Fig. 6.9.b), and probably only occur on the abaxial surface although it is difficult to show which fragments are of each surface given with the way the cuticle was prepared. Those organic fragments that do not preserve stomata probably represent the adaxial surface. The subsidiary cell arrangement for each stoma is unknown. Trichome bases are preserved on the surface and are both unicellular (Fig. 6.9.c) and multicellular (Fig. 6.9.d-e) in form. The multicellular trichome bases are interpreted here to be formed by numerous small cells with an emergent trichome that no longer remains in the fossil specimen (Fig. 6.9.d-e), homologous to those in extant species (cf. Fig. 6.5.f-g). The central insertion point of the trichome into the base is preserved (see arrow in Fig. 6.9.e).

The specimen can be assigned to *Weinmannia* with confidence on the combined presence of an imparipinnate leaf formed by lateral leaflets and an elongated terminal leaflet, a winged rachis between successive leaflets and trichomes with multicellular bases on the leaf surface. This latter feature distinguishes the fossil from those extant leaves of *Cunonia* species that have imparipinnate leaves with a winged rachis (e.g. *C. varijuga* and *C. pterophila*, Hoogland *et al.* 1997). The fossil probably represents an extinct *Weinmannia* species based on the very small size of the leaf and the lack of any serrations on the lateral leaflets (which have brochidodromous secondary venation), characters that have not been observed in any extant species examined in this study. However, the erection of a new fossil species is premature at this stage without further examination of extant material from South America which was limited for this study.

Figs 6.9.a-e. *Weinmannia* indet. sp. (specimen WC-236) from Wilson's Creek, central Tasmania.

Fig. 6.9.a. Macrofossil. All intact lateral leaflets have an entire margin while the apical portion of the terminal leaflet preserves several small teeth (arrow). Note the presence of a winged rachis between the leaflets. Scale bar = 3 mm.

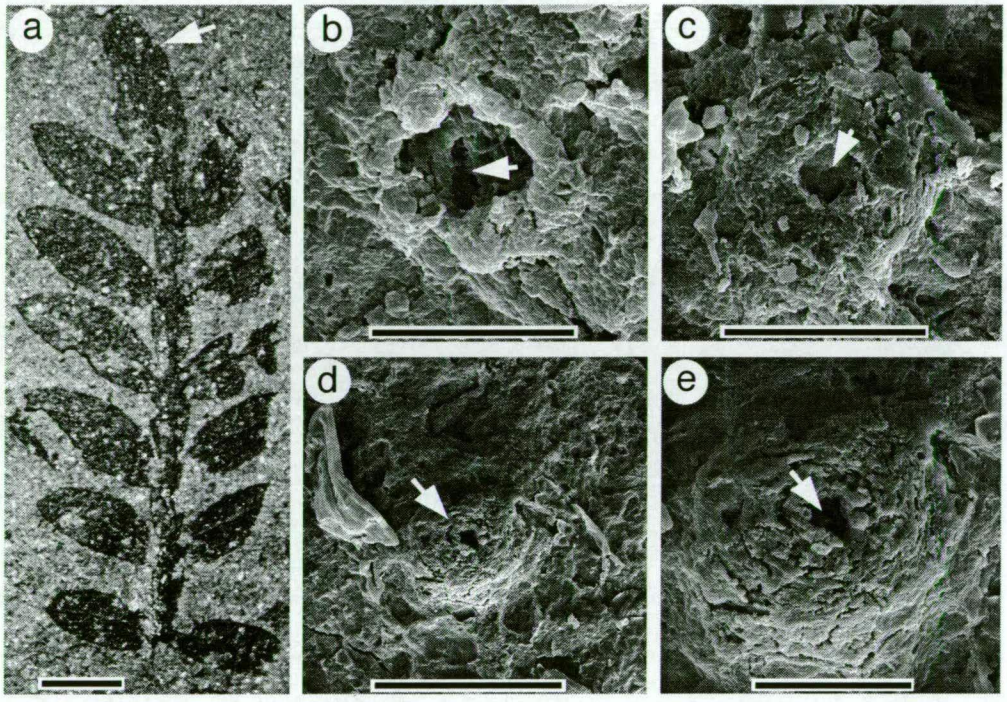
Figs 6.9.b-e. Scanning electron micrographs of the outer cuticle of specimen WC-236 showing surface features.

Fig. 6.9.b. A poorly preserved stoma on the ?abaxial surface. The arrow indicates the stomatal pore. Scale bar = 20 μm.

Fig. 6.9.c. Unicellular trichome base. The arrow indicates the insertion point of the trichome. Scale bar = 30 μm.

Fig. 6.9.d. Multicellular trichome base (arrow) on the ?adaxial surface. Scale bar = 100 μm.

Fig. 6.9.e. High magnification of the multicellular trichome base in figure 6.9.d. The arrow indicates the insertion point of the trichome. Scale bar = 50 μm.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This is the only leaf macrofossil that can definitively be assigned to the genus *Weinmannia.*

Petrified wood closely related to that of *Weinmannia* has been recovered from Cerro Bororo, Chubut in Argentina (Petriella 1972; Petriella and Archangelsky 1975). The fossil wood is Lower Tertiary (Paleocene) in age and has been described as two extinct species, *Weinmannioxylon pluriradiatum* and *W. multiperforatum* (Petriella 1972; see also Rancusi *et al.* 1987). Distinguishing the fossil wood from extant taxa and each other was conducted on the basis of pore density, which was found to be considerably less than that observed in extant species (Petriella 1972). Upper Cretaceous sediments from the Antarctic Peninsula have also been found to contain petrified wood of *Weinmannioxylon* (I. Poole pers. com.). More recent Late Pleistocene lake sediments from Ecuadorian Amazonia have also yielded wood fragments of the *Weinmannia*-type, although they may equally represent *Symplocos* or *Laplacea* (Bush *et al.* 1990). These wood records remain unverified as the original material was unavailable and the examination of fossil wood was beyond the scope of this study.

6.10.3 Discussion

The extant imparipinnate leaves of some *Weinmannia* species can be distinguished from those of extant *Cunonia* based on the presence of multicellular trichome bases (Table 6.1). However, in the absence of these, it would be difficult to identify macrofossils to either genus, unless the subsidiary cell arrangement was something other than anisocytic (the only form present in *Cunonia*). Those macrofossils without organic preservation that are similar to the imparipinnate leaves of *Cunonia* and *Weinmannia* can be placed in *Weinmanniaphyllum.* Dispersed leaves or leaf fragments may possibly be assigned to *Weinmannia* on the combined presence of multicellular trichome bases, tooth vascularisation, and subsidiary cell arrangement (see Table 6.1).

The affinity of X-it from New Zealand to *W. racemosa* is supported by cuticular morphology, and in particular the presence of multicellular hair bases (Fig. 6.5.h) homologous to those present in *W. racemosa.* The unilacunar nodes in X-it (Garnock-Jones *et al.* 1996) may have been reduced from the more common tri-lacunar condition in Cunoniaceae, which has also been suggested to have occurred within *Bauera* due to its overall reduced size (Dickison 1980*a*).

Table 6.1. Morphological features of extant *Weinmannia* and *Cunonia* species that may be useful in identifying leaf macrofossils

Characters in bold are those that are most useful in distinguishing between leaves of both genera. Note that it may not be possible to assign macrofossils to either genus if the fossil has a combination of characters that overlap between the genera. For example, leaf macrofossils with an anisocytic subsidiary cell arrangement that do not possess any multicellular trichome bases cannot be assigned to either genus with confidence (see text for further explanation).

Feature/structure	*Weinmannia*	*Cunonia*
Leaves	unifoliolate (simple?), trifoliolate, imparipinnate	unifoliolate (simple?), trifoliolate, imparipinnate
Secondary venation	craspedodromous to semicraspedodromous	craspedodromous to semicraspedodromous
Tertiary venation	reticulate	reticulate
Leaf margin	serrate	serrate, rarely entire
Sinus	glandular pubescent	glandular pubescent
Subsidiary cell arrangement	anomocytic, anisocytic, encyclocytic, brachyparacytic	anisocytic
Adaxial epidermis	not mucilaginous	mucilaginous ('star-like' epidermal cell configurations)
Multicellular trichome bases	present or absent	absent
Unicellular trichome bases	present/absent	present/absent

The most definitive macrofossil of *Weinmannia* is presented in this study. This *Weinmannia* macrofossil, combined with the leaf macrofossils from Cethana if they represent *Weinmannia*, is unambiguous evidence that the genus was present on the Australian continent in the past, having become extinct from it no earlier than the Early Oligocene. The Early Miocene reproductive structure assigned to ?*Weinmannia* sp. indet. shows the presence of additional *Weinmannia* species, of sections other than Leiospermum, in New Zealand in the recent past.

6.11 Indeterminate Genera

6.11.1 Berwick Quarry, Victoria

Numerous Berwick Quarry leaf macrofossils have been considered by Pole *et al.* (1993) to have affinities with Cunoniaceae (see illustrations in Pole *et al.* 1993), and were divided into two taxa. One taxon of two specimens, ?Cunoniaceae sp. 'small teeth', are microphylls with craspedodromous venation. The second taxon, ?Cunoniaceae sp. 'lanceolate', has lanceolate shaped leaves with serrate margins and probably represent leaflets from a compound leaf as the macrofossils either have an asymmetrical or symmetrical base. These two taxa co-occur with macrofossils of *Callicoma serratifolia* and another possible Cunoniaceae genus (see Chapter 4 this study).

At present, the assignment of these macrofossils to any extant genus of Cunoniaceae is premature. No combination of architectural and cuticular features present in the fossils suggest a direct link to an extant genus of Cunoniaceae. Tentatively, the leaves may represent those of a *Weinmannia* species because of their general structure, however there are no substantial data at present to warrant such an identification. The leaves are therefore of unknown affinity.

6.11.2 Hasties, north-eastern Tasmania

The Hasties macrofossils described as ?Cunoniaceae Genus et species indet. by Pole (1992) are small leaf fragments with a serrate margin that possess a general cuticle without any distinguishing features. The stomates are of the anomocytic type and each trichome base has a radially flanged foot cell (see illustrations in Pole 1992). No features of the leaf architecture, combined with cuticular morphology, directly link it to

any extant genus of Cunoniaceae so the exact affinities of these macrofossils remain unknown.

Chapter 7. General Discussion

7.1 Verified Macrofossils of Cunoniaceae

After the extensive revision undertaken here it is evident that the Cunoniaceae has an extensive fossil record. Eleven of the 26 genera are represented as macrofossils including leaves or leaf fragments, dispersed cuticle, flowers and fruits or a combination of these (Table 7.1). Two genera are exclusively represented by reproductive structures (*Ceratopetalum* and *Schizomeria*), six genera are represented by both vegetative and reproductive organs (*Acsmithia, Bauera, Callicoma, Ceratopetalum, Eucryphia, Weinmannia*) and three are represented by leaves or leaf fragments alone (*Anodopetalum, Codia, Vesselowskya*). Leaves and reproductive structures of *Callicoma* and *Eucryphia* co-occur in two deposits. Most wood fossils are considered to be dubious and in need of more detailed revision. The three *Weinmannioxylon* species from Antarctica and Argentina (Chapter 6) are potentially significant given the age of the sediments (Early Paleocene-Eocene) and their geographic location but need more evidence to support their affinities to *Weinmannia.* Cunoniaceae genera that are not represented in the macrofossil record may have organs preserved within a fossil deposit but have simply not yet been located and identified.

All the accepted macrofossils of Cunoniaceae are from Australian Cainozoic deposits with the exception of a single infructescence from New Zealand (?*Weinmannia* sp. indet.). The macrofossils from New Zealand, Antarctica and South America are either misinterpreted as Cunoniaceae or excluded from this study as too little data are preserved in the original specimen, or in the illustration and description provided by the original author, to warrant any identification to the Cunoniaceae. Taxa considered to be indeterminate in Chapter 6 are also excluded until more satisfactory identifications are made. The macrofossils assigned to the Cunoniaceae from the Northern Hemisphere (e.g. Unger 1866; Ettingshausen 1888) are (i) no longer considered to represent the family (see Mai 1995), (ii) excluded from further discussion on the basis that the leaf architecture is not consistent with extant Cunoniaceae or (iii) too little data are preserved within the fossil itself to make any identification with confidence. The affinities of these latter fossils may lie with those families that occur within Europe, North America and Asia (e.g. see Mai 1995). Those macrofossils that are either doubtful or completely rejected as representing Cunoniaceae are discussed throughout the body of this thesis (also compare Tables 1.2

Table 7.1. Accepted macrofossils of Cunoniaceae genera

Genus or category	Species	Macrofossil type	Geological age	Site Locality	Source
Acsmithia	*grandiflora*	Flower	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
Anodopetalum	*biglandulosum*	Leaves with cuticle	Late Pleistocene	Melaleuca Inlet, Tasmania	Jordan *et al.* (1991)
Bauera	*rubioides*	Leaf with cuticle	Late Pleistocene	Melaleuca Inlet, Tasmania	Jordan *et al.* (1991)
		Immature capsule			This study (Chapter 6)
Bauera	*rubioides*	Leaves	Early to Middle Pleistocene	Regatta Point, Tasmania	Jordan *et al.* (1995)
Bauera	*rubioides*	Leaves	Holocene	Moxon Saddle, Tasmania	Warren (1994)
Callicoma	*serratifolia*	Leaves with cuticle	Early Oligocene	Lemonthyme Creek, Tasmania	This study (Chapter 4)
Callicoma	*serratifolia*	Leaves with cuticle	Early Oligocene	Little Rapid River, Tasmania	This study (Chapter 4)
		Infructescences (2)			
Callicoma	*serratifolia*	Leaves with cuticle	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
		Infructescence			This study (Chapter 4)
		Seeds with coat			
Callicoma	*serratifolia*	Leaves with cuticle	Late Oligocene	Berwick Quarry, Australia	This study (Chapter 4)
Callicoma	*serratifolia*	Leaf impressions	Miocene to Pliocene	Stuart Creek, South Australia	This study (Chapter 4)
Codia	*australiensis*	Mineralised leaf	Middle Eocene-Oligocene	West Dale, Australia	This study (Chapter 4)

Table 7.1. continued. Accepted macrofossils of Cunoniaceae genera

Genus or category	Species	Macrofossil type	Geological age	Site Locality	Source
Ceratopetalum	*priscum*	Fruit compression	Middle Miocene	Chalk Mountain Formation, Australia	Holmes and Holmes (1992)
Ceratopetalum	*westermannii*	Fruit compressions	late Early-Late Miocene	Elands, Australia	This study (Chapter 3)
Ceratopetalum	*wilkinsonii*	Fruit compression	Late Eocene-Early Oligocene	Vegetable Creek, Australia	Holmes and Holmes (1992)
Ceratopetalum	*maslinensis*	Fruit compressions	Middle Eocene	Maslin Bay, South Australia	This study (Chapter 3)
Eucryphia	*aberensis*	Mummified leaves	Late Eocene	Loch Aber, Tasmania	Hill (1991*a*) This study (Chapter 5)
Eucryphia	*aberensis*	Leaves with cuticle	Early Oligocene	Little Rapid River, Tasmania	This study (Chapter 5)
Eucryphia	*falcata*	Leaf compressions	Late Paleocene	Lake Bungarby, Australia	Hill (1991*a*)
Eucryphia	*leaensis*	Leaf with cuticle	Early Oligocene	Lea River, Tasmania	This study (Chapter 5)
Eucryphia	*lucida*	Leaves	Middle to Late Pleistocene	Pieman Dam, Tasmania	Colhoun (1980)
Eucryphia	*lucida*	Leaves	Early Pleistocene	Regatta Point, Tasmania	This study (Chapter 5)
Eucryphia	*milliganii* ssp. *milliganii*	Leaves	Early Pleistocene	Regatta Point, Tasmania	This study (Chapter 5)
Eucryphia	*lucida*	Leaves	Middle Pleistocene	Regency Formation, Tasmania	Fitzsimons *et al.* (1990); Jordan (1992), Taylor (1993)
Eucryphia	*milliganii* ssp. *milliganii*	Leaves	Middle Pleistocene	Regency Formation, Tasmania	This study (Chapter 5)
Eucryphia	*mucronata*	Leaf with cuticle	?Latest Eocene-Early Oligocene	Wilson's Creek, Tasmania	This study (Chapter 5)
Eucryphia	*reticulata*	Capsule	Early Oligocene	Lea River, Tasmania	This study (Chapter 5)

Table 7.1. continued. Accepted macrofossils of Cunoniaceae genera

Genus or category	Species	Macrofossil type	Geological age	Site Locality	Source
Eucryphia	sp. 'LRR1'	Incomplete capsule	Early Oligocene	Little Rapid River, Tasmania	This study (Chapter 5)
Eucryphia	sp. 'Leven'	Dispersed cuticle	Early Oligocene	Leven River, Tasmania	This study (Chapter 5)
Eucryphia	sp.	Dispersed cuticle	Early to Middle Pleistocene	Regatta Point, Tasmania	Jordan *et al.* (1995)
Eucryphia	sp.	Dispersed cuticle	Late Pleistocene	Melaleuca Inlet, Tasmania	Jordan *et al.* (1991)
Schizomeria	*tasmaniensis*	Flower	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
Spiraeanthemum/Acsmithia		Dispersed cuticle	late Middle Eocene	Western Australia	Carpenter and Pole (1995)
Spiraeanthemum/Acsmithia		Dispersed cuticle	late Middle Eocene to early Late Eocene	South Australia	This study (Chapter 6)
Vesselowskya	aff. *rubifolia*	Leaf with cuticle	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993)
Weinmannia	sp. indet.	Leaf with cuticle	?Latest Eocene-Early Oligocene	Wilson's Creek, Tasmania	This study (Chapter 6)
?Weinmannia	sp. indet.	Infructescence	Early Miocene	Manuherikia Group, New Zealand	Pole (1993*b*) This study (Chapter 6)
Weinmanniaphyllum	*bernardii*	Leaf impressions	Early Oligocene	Cethana, Tasmania	Carpenter and Buchanan (1993) This study (Chapter 6)

and 7.1).

The number of extant genera represented in the macrofossil record of the Cunoniaceae is high (42% of extant genera, Table 7.1) compared to that in the macrofossil record of other Southern Hemisphere flowering plant families, including Proteaceae, Lauraceae and Nothofagaceae. Despite the abundance of Proteaceae macrofossils only a few have been assigned to an extant genus, with the majority in the fossil genus *Euproteaciphyllum* (e.g. Carpenter and Jordan 1997; Jordan *et al.* 1998). Similarly, most Lauraceae are either identified as the extant genus *Cinnamonum* or are placed into the fossil genus *Laurophyllum* (e.g. Hill 1986, 1988). Therefore, in comparison to these families, this study demonstrates that macrofossils of Cunoniaceae can in most cases be confidently assigned to an extant genus, and with this brings an opportunity to better examine intra-familial evolution and biogeography. Nothofagaceae has an extensive and well documented fossil record (e.g. Hill 1983*a*, 1983*b*, 1991*b*, 1994; Hill and Dettman 1996), however this family only contains a single genus, *Nothofagus*, composed of four subgenera (see Hill and Read 1991) which have all been identified as macrofossils. The occurrence of 11 of the 26 extant Cunoniaceae genera in the macrofossil record possibly indicates that the Cunoniaceae were conspicuous elements in the Cainozoic flora or, at the least, frequently occurred near a site of deposition.

7.2 Fossil Evidence For Palaeogeography And Extinctions

Macrofossils of rainforest and wet forest Cunoniaceae genera, including *Acsmithia, Schizomeria, Callicoma* and *Vesselowskya*, show that they were present in southern, south-eastern or south-western Australia during the Early Cainozoic. The palaeogeographic distribution of these taxa probably reflects the presence of suitably wet and aseasonal environments in those areas of Australia at that time (e.g. Sluiter 1991; Quilty 1994), and is supported by co-occurring taxa that generally inhabit rainforest environments, including *Nothofagus*, Araucariaceae, Podocarpaceae and *Gymnostoma* (e.g. Carpenter and Pole 1995; Hill and Carpenter 1991; Hill 1991*b*, 1995). The overall floristic similarities of Palaeogene fossil floras to those of extant high rainfall microthermal and mesothermal habitats has been noted by several authors (e.g. Carpenter *et al.* 1994; Christophel 1994), and probably indicates that climatically similar rainforest environments occurred in at least parts of Australia during that time.

The regional extinction or retraction of many Cunoniaceae genera into their current

geographic ranges can probably best be explained by the development and expansion of climatically unsuitable habitats in central and southern areas of Australia during the Cainozoic (e.g. Truswell 1993; Quilty 1994; Macphail *et al.* 1994). A similar hypothesis has been suggested to explain the extinction or geographic retraction of other rainforest genera in Australia, including *Gymnostoma* (Hill 1994), *Acmopyle* and *Dacrycarpus* (Hill and Carpenter 1991) and subgenera of *Nothofagus* (Hill 1983*b*). More specifically, climates have been suggested to have become drier, more seasonal, colder, or a combination of these (e.g. Macphail *et al.* 1994) and were of sufficient magnitude and severity to remove many taxa that now have their nearest living relatives in micro- and mesothermal rainforest environments of New Caledonia and Papua New Guinea (e.g. Hill 1983*b*).

The fossil pollen record of Cunoniaceae was not directly examined as part of this study it was largely beyond the scope of this review, with the records presented in this thesis drawn exclusively from previous literature. Although the Cunoniaceae pollen record is at a low taxonomic resolution, previous studies show that all three Cunoniaceae pollen types (see Table 1.3) once occurred in South Australia (Late Paleocene, Sluiter 1991; Oligocene-Miocene, Truswell *et al.* 1995), Victoria (Eocene, Stover and Partridge 1973; Oligo-Miocene, Blackburn and Sluiter 1994) and Tasmania (Oligocene, Hill and Macphail 1983). Dicolporate pollen genera still occur in some of these areas (e.g. *Bauera, Anodopetalum, Eucryphia*) but tricolporate pollen genera have become restricted to wet forest habitats in eastern Australia (New South Wales and Queensland) or overseas (see Table 1.1 and 1.3). The extinction of the syncolpate and tricolporate pollen types supports the trend in regional extinctions demonstrated by the macrofossil record. Tricolporate Cunoniaceae pollen occurred in western Tasmania as recently as the Late Pliocene (Macphail *et al.* 1995) and probably marks not only the Tasmanian extinction of one or more genera of Cunoniaceae (see Table 1.3) but also that of *Nothofagus* subgenus *Brassospora*, *Beauprea* (Proteaceae), Araucariaceae and (Macphail *et al.* 1995). The extinction of these taxa was probably related to the onset of glacial climates (cold and dry) during the Pleistocene (Macphail *et al.* 1995).

It is difficult to interpret the continental extinction of some genera as the direct result of a changing climate. Instead, temporal changes in other natural processes, including shifts in geological and/or ecological processes, may have driven these extinctions and are perhaps independent of climatic effects. *Weinmannia* is widely distributed today in a variety of habitat types and climatic zones (Hopkins 1998*a*) on land masses geographically close to Australia, including New Zealand, New Caledonia, Papua New Guinea and some Pacific Islands (Bradford 1998). Given the diversity of

habitats occupied by the genus today it is very difficult to hypothesise that the extinction of *Weinmannia* in Australia was due to the lack of climatically suitable habitats in part.

As most *Weinmannia* species have a disturbance based ecology (Wardle 1966; Veblen *et al.* 1981; Stewart 1986), where catastrophic events are important for regeneration (e.g. *W. racemosa*, Stewart and Veblen 1982), a cessation of large scale landscape processes, such as volcanism, landslips and uplifting, may have stopped or reduced the frequency of vegetation disturbance. Thus, the extinction of *Weinmannia* in Australia may have been due to the loss of its regeneration niche. This is similar to the explanation provided for the Australian extinction of *Nothofagus* subgenus *Nothofagus* (Hill 1991*b*; Scriven and Hill 1996) and *Fitzroya* (Hill and Whang 1996). This hypothesis is supported by the current absence of *Weinmannia* from low lying geologically inactive coralline islands in the Pacific but its widespread and occasional abundance on volcanic islands where landslips and volcano induced disturbances are common (Hopkins 1998*a*). This life cycle characteristic may also account for its abundance in the volcanic regions of South and Central America, especially along the Ecuadorian and Colombian Andes (Bradford 1998).

This hypothesis is however complicated by two factors. Not all extant species of *Weinmannia* require disturbance for regeneration, as some will regenerate under an existing canopy (e.g. Hopkins 1998*a*). In addition, a source of catastrophic disturbance, in the form of volcanism, has been present in the Australian landscape throughout the Cainozoic and, in some regions of Australia, until quite recently (see Quilty 1994). However, due to the sporadic temporal and geographic nature of these events in Australia suitable habitats for *Weinmannia* may not have been continually present during the Cainozoic.

It is difficult to formulate a hypothesis for the cause of the continental extinction of some genera, including *Codia* in Australia and *Gillbeea* (*Concolpites leptos* pollen type) in South America (Romero and Castro 1986). Based on the extant habitat and climatic range of both these genera it is difficult to invoke climate change as a principal factor as it is likely that suitable climates for both were present on these landmasses in the past. Extinctions are probably complex processes that cannot always be attributed to a single factor such as climate change. The ability to formulate hypotheses to explain some extinctions is also complicated by the lack of any fossil evidence of factors that may have actually been instrumental in the process, such as a loss of pollination or dispersal vector, a high level of genetic inbreeding or a local catastrophic

event such as fire. Additional information on the life history characteristics of *Codia* and *Gillbeea* genera, which is largely lacking, may enable a more accurate assessment of their extinction to be made.

7.3 Minimum Family And Generic Age

The fossil record combined with the revised phylogeny of the Cunoniaceae by Bradford and Barnes (manuscript submitted, Appendix 1) allows minimum ages to be placed onto clades and some genera within the family (Fig. 7.1; Table 7.2). *Eucryphia falcata* from the Late Paleocene of Australia provides a minimum age for a node deep in the phylogeny of the family (Fig. 7.1) and implies that the ancestors to the genera basal to *Eucryphia* were present in the vegetation no later than the Late Paleocene. This hypothesis is supported by the minimum age of other genera deeply nested within the phylogeny (Fig. 7.1), including *Codia* (Middle Eocene-Early Oligocene), *Weinmannia* (latest Eocene-Early Oligocene), *Callicoma* (Early Oligocene) and *Vesselowskya* (Early Oligocene). Furthermore, *Weinmannia* may have a Late Paleocene origin based on fossil pollen from Seymour Island (cf. *Weinmannia*, Cranwell 1959) and Argentina (*Rhoipites* sp. aff. *Weinmannia*, Petriella and Archangelsky 1975). As a result, this macrofossil evidence suggests that generic diversification was more or less complete by the Early Cainozoic.

Based on the minimum age of many extant Cunoniaceae genera, it is reasonable to hypothesise that the Cunoniaceae originated in the late Cretaceous or earlier. This is not improbable given the hypotheses that other widespread Southern Hemisphere families originated in the mid (Proteaceae, Hoot and Douglas 1998) to late Cretaceous (Nothofagaceae, Hill and Dettman 1996). However, unlike these families there is no macrofossil or pollen evidence to support an age of the Cunoniaceae older than the Late Paleocene. Cunoniaceae pollen at least may be present in Cretaceous sediments but has simply not been detected due to its small size, lack of distinguishing features or its similarity with the pollen of other families, including the Elaeocarpaceae which are the sister group to the Cunoniaceae (Fig. 7.1).

The Paleocene origin of some plant groups and the close proximity of the continents at this time may account for their equilibrated worldwide or Southern Hemisphere distribution (Romero 1993). This hypothesis may explain the widespread Southern Hemisphere distribution of Cunoniaceae genera and the apparent geographic disjunctions for some genera. Although a Late Paleocene age at least is supported for the origin of the Cunoniaceae it is unlikely, for example, that the disjunct distribution

Table 7.2. Minimum geological age for genera of Cunoniaceae based on accepted macrofossils of the family

Those genera with confirmed macrofossil records are included in this summary (see Table 7.1). Fossil pollen, with the exception of *Concolpites leptos* (*Gillbeea* type), were excluded from this summary as they remain unverified or are at a low taxonomic resolution.

Taxon	Minimum geological age
Eucryphia	Late Paleocene
Codia	Middle Eocene-Oligocene
Spiraeanthemum/Acsmithia [A]	late Middle Eocene
Ceratopetalum	Middle Eocene
Gillbeea (*Concolpites leptos* pollen type)	Eocene
Acsmithia	Early Oligocene
Callicoma	Early Oligocene
Schizomeria	Early Oligocene
Vesselowskya	Early Oligocene
Weinmanniaphyllum [B]	Early Oligocene
Weinmannia	Latest Eocene-Early Oligocene
Bauera	Early to Middle Pleistocene
Anodopetalum	Late Pleistocene

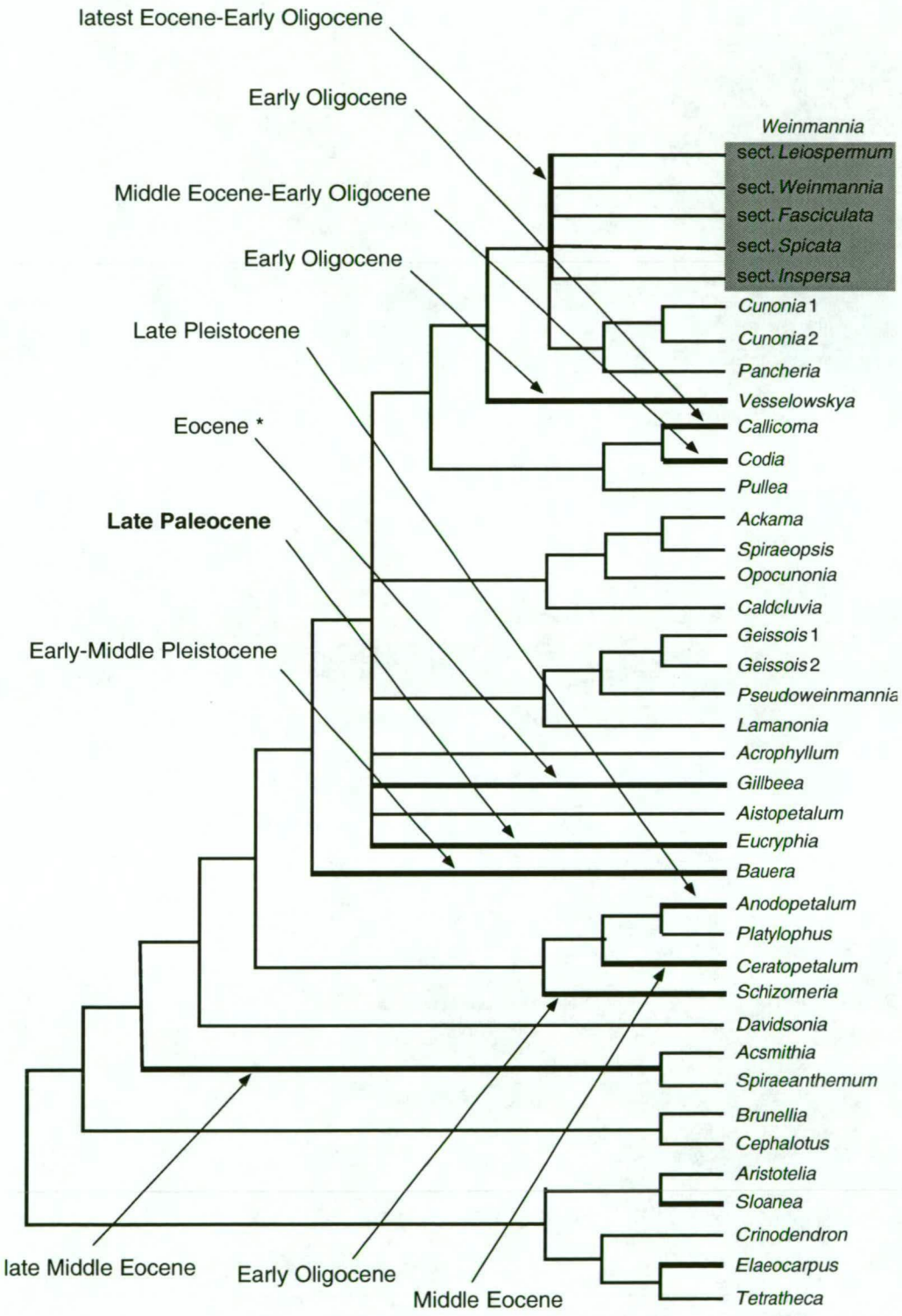
Key: [A] dispersed cuticle unassignable to either genus with confidence; [B] form genus that contains imparipinnate fossil leaves that are indistinguishable from those of some extant *Cunonia* and *Weinmannia* species.

Fig. 7.1. Minimum generic age for those genera with a fossil record overlayed onto the phylogeny of the Cunoniaceae. The cladogram is a strict consensus tree produced from a parsimony analysis of morphological characters at the generic level for Cunoniaceae and outgroup genera using a constraint tree based on clades supported by molecular data (see Bradford and Barnes manuscript submitted, Appendix 1).

The minimum age for each genus (shown by arrows and geological age) is derived from the accepted macrofossil record of the family (see Table 7.1). This is with the single exception of *Gillbeea* (marked by an asterix) which is represented by the pollen type *Concolpites leptos* in Argentina (Eocene, Romero and Castro 1986) and Australia (Eocene to Early Oligocene, Stover and Partridge 1973).

Geissois was separated into two terminal taxa, with each containing the species of Australia (*Geissois* 1) or the Pacific (*Geissois* 2). *Cunonia* was also separated into two terminal taxa, one containing most species in the genus (*Cunonia* 1) and the other the South African *C. capensis, C. macrophylla* and *C. schiziana* on the basis of andromonecy (*Cunonia* 2). Each section of *Weinamnnia* represents a terminal taxon, with the floral and leaf morphological features of each section, and the species that they contain, defined by Bradford (1998). See Bradford and Barnes (manuscript submitted, Appendix 1) for more details of each terminal taxon.

Leaf macrofossils with affinities to Elaeocarpaceae (*Sloanea/Elaeocarpus*, Eocene Golden Grove, Christophel and Greenwood 1987; Elaeocarpaceae, late Middle Eocene Angelsea, Christophel *et al.* 1987; see Fig. 2.1 for deposit locations), which is represented in the cladogram by two outgroup genera, have been recovered from Australian fossil deposits. Fossil fruits of *Elaeocarpus* have also been described (Early to Middle Miocene, Rozefelds and Christophel 1996).


latest Eocene-Early Oligocene
Early Oligocene
Middle Eocene-Early Oligocene
Early Oligocene
Late Pleistocene
Eocene *
Late Paleocene
Early-Middle Pleistocene
late Middle Eocene
Early Oligocene
Middle Eocene
Weinmannia
sect. Leiospermum
sect. Weinmannia
sect. Fasciculata
sect. Spicata
sect. Inspersa
Cunonia 1
Cunonia 2
Pancheria
Vesselowskya
Callicoma
Codia
Pullea
Ackama
Spiraeopsis
Opocunonia
Caldcluvia
Geissois 1
Geissois 2
Pseudoweinmannia
Lamanonia
Acrophyllum
Gillbeea
Aistopetalum
Eucryphia
Bauera
Anodopetalum
Platylophus
Ceratopetalum
Schizomeria
Davidsonia
Acsmithia
Spiraeanthemum
Brunellia
Cephalotus
Aristotelia
Sloanea
Crinodendron
Elaeocarpus
Tetratheca

of *Cunonia* in southern Africa and New Caledonia and *Weinmannia* in Madagascar and the Pacific and Americas represents vicariance. This scenario would require these genera to be at least 120 to 140 million years old (Early Cretaceous) as this is approximately when Africa started to break away from Gondwana (Quilty 1994). Given the position of *Cunonia* and *Weinmannia* in the phylogeny of the Cunoniaceae (Fig. 7.1) this would then imply that all the ancestors to the extant genera were present in the vegetation. However, this is unlikely as it would then be expected that more genera would have an equilibrated Southern Hemisphere distribution, unless there has been a significant number of continental extinctions since the mid to late Cretaceous. Although an Early Cretaceous origin for the Cunoniaceae is not impossible, it is a hypothesis that requires additional evidence from the fossil record and/or molecular clock data, as has been conducted for *Nothofagus* (Martin and Dowd 1993).

An alternative and more plausible hypothesis to explain the geographic disjunctions in Cunoniaceae genera is that long-distance dispersal has occurred whereby propagules have dispersed between continents after the breakup of Gondwana. Dickison (1984) notes that numerous Cunoniaceae genera have small winged seeds that are probably dispersed by wind, with some fleshy indehiscent fruits perhaps dispersed by water or animals. Therefore, it is not improbable that some of the genera with small winged seeds are capable of dispersing across small distances between land masses with the aid of storms and cyclones. Long-distance dispersal has only relatively recently been proposed as a means to explain the extant biogeography of some plant groups (e.g. *Nothofagus*, Martin and Dowd 1993) even though it is a hypothesis well supported by fossil evidence (see Hill and Dettman 1996). Pole (1994) even comments that the entire New Zealand flora may actually represent the final result of long-distance dispersal events.

For the Cunoniaceae, Bradford (1998) suggests that a sister taxa relationship between some *Weinmannia* species in the Americas and those that occur in the Mascarenes (near Madagascar) would be best explained by a dispersal event rather than by vicariance. Long-distance dispersal of *Weinmannia* today is important for the colonisation of new volcanic offshore islands in the South Pacific region (Hopkins 1998*a*) and there is no reason to suggest that this extant phenomenon was less important in the past. Based on the location and age of *Codia australiensis*, it is possible that *Codia* dispersed from Australia to New Caledonia or vice versa, with subsequent extinction of it from the former land mass. *Platylophus* and *Cunonia* have their nearest relatives in the Australia-Pacific region and may have dispersed from there in a single event or via other continents in a series of dispersal events. Additional

macrofossils of either genus from Africa or South America in particular may provide evidence for this. Experiments subjecting Cunoniaceae seeds to salt water for prolonged periods of time may enable a more detailed assessment of seed viability to be made after exposure to salt water.

7.4 Evolutionary Trends In The Cunoniaceae

7.4.1 Leaf Morphology

Trends in foliar evolution through Cainozoic have been widely documented for other genera in Australia, including *Acmopyle* and *Dacrycarpus* (Hill and Carpenter 1991), *Nothofagus* (Hill 1983*b*, 1994) and Casuarinaceae (Hill 1994). Most of the evolutionary trends that have been identified include temporal changes in one or a combination of morphological traits, such as a reduction in leaf size or an increase in the level of protection offered to the stomata (e.g. occurrence in pits). In most cases, this foliar evolution has been interpreted to be a response to Cainozoic climate change. For example, Hill and Carpenter (1991) interpret leaf reduction and a change in phyllotaxy, combined with a restriction in the distribution of stomata in *Acmopyle* and *Dacrycarpus* to represent adaptations to prevent water loss in a drying environment.

There have been few general trends in the evolution of leaf form across the Cunoniaceae, with the exception of leaf or leaflet reduction and the development of adult leaves with entire margins within several different clades (e.g. Hufford and Dickison 1992; Bradford and Barnes manuscript submitted, Appendix 1). Macrofossils of specific genera do provide evidence of intra-generic foliar evolution, most notably in *Eucryphia.* Trends identified in the macrofossil record of *Eucryphia* include a reduction in leaflet number, the development of an entire leaf margin and the evolution and continued development of peltiform cuticular extensions through the Cainozoic (see Fig. 5.15). The extensions in *Eucryphia* could be interpreted as being xeromorphic, as defined by Hill (1998) for the Proteaceae, as they conceivably protect individual stomata and increase the boundary layer to prevent water loss. However, reducing water loss is unlikely to have been the initial role of these structures when they first arose in *E. falcata* or its ancestor as the suggested palaeoclimate of Lake Bungarby (Late Paleocene) was probably wet and relatively aseasonal (Taylor *et al.* 1990). Instead, the extensions may have arisen to prevent water accumulation on the leaf which can occur in everwet environments (Hill 1998). Once evolved, it is plausible that these cuticular extensions were an exaption to the cooler and drier climates of the Middle to Late Cainozoic whereby they increased the boundary layer to

reduce water loss and prevented ice crystal formation across the leaf surface.

In contrast, the foliage of *Callicoma* has remained relatively unchanged since the Early Oligocene. The absence of leaf dimorphism in *Callicoma* may be due to its proposed paedomorphic origin from a common ancestor with *Codia*, which is supported by the phylogeny of the tribe Codieae (Fig. 4.18). *Callicoma* and two species of *Codia* have dense paired trichomes on the abaxial surface and a cutin frill or ledge surrounding each stoma. Hill (1998) proposes that for the Proteaceae at least that dense trichomes and cuticular ledges around the stomatal pore initially arose in everwet environments to prevent water accumulation on the leaf surface and in the stomatal pore. Brewer and Smith (1997) specifically identify dense trichomes as being able to keep water away from the leaf surface thus enabling stomata to be unobscured. The trichomes and cutin frill may have arisen in the ancestor to *Callicoma* and *Codia* as a response to low nutrient soils and high rainfall habitats, such as that proposed for West Dale (see Hill and Merrifield 1993) where *Codia australiensis* occurs. It is possible that these adaptations, in addition to the retention of serrate leaves, in *Callicoma* has some adaptive advantage over those entire margin leaves of the ancestor, or those of extant *Codia*, however the exact advantage is unknown.

Clearly within the Cunoniaceae, *Eucryphia* at least follows the general trends of leaf reduction and stomatal protection identified in other families such as Podocarpaceae (*Acmopyle* and *Dacrycarpus*, Carpenter and Hill 1991). Therefore, this evidence from the Cunoniaceae further supports the hypothesis of Hill and Carpenter (1991) that there has been convergent evolution in leaf form in response to climate change among various conifer and angiosperm families.

In some instances, the evolution of leaf form within Cunoniaceae genera may not have been driven by climate change, but rather may be an artefact of substrate chemistry. It is generally accepted that soil nutrition and chemistry can play a key role in generic and species diversification, including the evolution of scleromorphy (low protoplasm to lignin content in leaves) in the Australian vegetation in response to low phosphorus levels (Loveless 1961, 1962; Beadle 1966) and the rapid radiation of some plant groups growing on the ultramafic substrates in New Caledonia, including *Araucaria* (Setoguchi *et al.* 1998) and *Nothofagus* subgenus *Brassospora* (Setoguchi *et al.* 1997). Most Cunoniaceae inhabit highly oligotrophic substrates (e.g. Floyd 1989) and are generally scleromorphic in leaf form. In New Caledonia many genera of Cunoniaceae grow on ultramafic soils and have thick leaves with at least one species, *Geissois pruinosa*, accumulating heavy metals in its foliage (Jaffré *et al.* 1979). More

detailed studies on intra-generic relationships within New Caledonian genera and their growing substrates may provide support to the hypothesis of rapid radiation or unique morphologies as a response to novel soil chemistries.

7.4.2 Floral Morphology

As very few Cunoniaceae reproductive structures are preserved or identified it is difficult to make a macrofossil based assessment of the evolution of floral form in the family. Flowers of *Acsmithia grandiflora* and *Schizomeria tasmaniensis* are larger than any of their close living relatives. Dickison (1989) suggests that floral reduction and a loss of petals within the primitive Rosidae may have been associated with a shift in pollination vector from entomophily to partial or exclusive anemophily. Therefore, based on this hypothesis and the macrofossil record, this shift had not occurred by the Early Oligocene in *Acsmithia* and *Schizomeria* but the secondary loss of petals in *Ceratopetalum* had occurred as early as the Middle Eocene. This loss of petals, and strong development of basally constricted lobed sepals may have been evolutionary advancements to improve seed aerodynamics as they are wind dispersed (Dickison 1984).

The prevalence of bicarpellate fruits in Cunoniaceae is well documented, with the development of multicarpellate fruits in *Eucryphia* at least (e.g. Hufford and Dickison 1992; Bradford and Barnes manuscript submitted, Appendix 1). *Eucryphia reticulata* and *E.* sp. 'LRR1' support an early occurrence of multicarpellate fruits in the genus (Early Oligocene), most likely with a secondary reduction in carpel number observed in some extant species (e.g. *E. lucida* and subspecies of *E. milliganii*, Taylor and Hill 1996).

7.5 Conclusions

The fossil record of Cunoniaceae confirms an ancient origin of the family, with generic diversification probably complete by the Early Cainozoic. Within Australia there has been regional and continental extinctions, most likely due to climatic changes or periods of geological quiescence, although for others the cause remains unknown. The extant biogeography of most genera can be explained by vicariance while for others long-distance dispersal events must be considered to have occurred, particularly for those genera in Africa and Madagascar.

Australia has many unstudied fossiliferous deposits that contain leaf and reproductive macrofossils. Further research on these deposits, and others that occur overseas, may yield additional Cunoniaceae macrofossils to enhance our understanding further on the families biogeographic history. Furthermore, the examination of the Cunoniaceae fossil record, combined with that of Elaeocarpaceae, may provide additional information on the evolutionary trends that have occurred within these two closely related families.

Chapter 8. References

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Appendix 1. Publications and manuscripts in press.

Barnes, R. W., and Hill, R. S. (1999*a*). *Ceratopetalum* fruits from Australian Cainozoic sediments and their significance for petal evolution in the genus. *Australian Systematic Botany* **12**, 635-645 (see back of thesis).

Barnes, R. W., and Hill, R. S. (1999*b*). Macrofossils of *Callicoma* and *Codia* (Cunoniaceae) from Australian Cainozoic Sediments. *Australian Systematic Botany* **12**, 647-670 (see back of thesis).

Barnes, R. W., and Jordan, G. J. (2000). *Eucryphia* (Cunoniaceae) reproductive and leaf macrofossils from Australian Cainozoic sediments. *Australian Systematic Botany* **13**

Barnes, R. W., and Rozefelds, A. C. (2000). Comparative morphology of *Anodopetalum* (Cunoniaceae). *Australian Systematic Botany* **13**

Bradford, J. C., and Barnes, R. W. (manuscript submitted). Phylogenetics of the Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Systematic Botany*

Eucryphia (Cunoniaceae) Reproductive and Leaf Macrofossils from Australian Cainozoic Sediments

Running title: *Eucryphia* Macrofossils from Cainozoic Sediments

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Abstract

The first fossil capsule of *Eucryphia*, *E. reticulata* R.W.Barnes & G.J.Jord. sp. nov., is described from Lea River (Early Oligocene), and, like capsules of the two extant South American species *E. glutinosa* (Poepp. et Endl.) Baill. and *E. cordifolia* Cav., is large and has a relatively large number of valves. The capsule occurs with a *Eucryphia* leaf macrofossil that was probably a leaflet from a compound leaf as it is highly falcate. The leaflet may be derived from the same parent plant as *E. reticulata* but in the absence of an organic connection it is described as a new species, *E. leaensis* R.W.Barnes & G.J.Jord. sp. nov. Additional leaf macrofossil specimens of *E. aberensis* from the type locality (Loch Aber; Middle to Late Eocene) and a new locality record for the species, Little Rapid River (Early Oligocene), indicate that the species had compound leaves formed by serrate and entire margin leaflets. Another incomplete *Eucryphia* capsule occurs at Little Rapid River (Early Oligocene) but it is too poorly preserved to assign it to an extant or extinct species. It may be derived from the same parent plant as *E. aberensis* R.S. Hill, with which it occurs, but cannot be confirmed as there is no organic connection. A new leaf macrofossil with serrate margins, *E. mucronata* R.W.Barnes & G.J.Jord., sp. nov., is also described from ?Latest Eocene-Early Oligocene sediments at Wilsons Creek, central Tasmania. Leaf macrofossils previously assigned to *E.* aff. *milliganii* from Early Pleistocene sediments at Regatta Point in western Tasmania are shown to be conspecific with the two extant Tasmanian species, *E. lucida* (Labill.) Baill. and *E. milliganii* Hook.f. ssp. *milliganii* based on foliar hair distribution patterns and density. The oldest fossil *Eucryphia* species, *E. falcata* R.S. Hill (Lake Bungarby; Late Paleocene), had compound leaves formed by leaflets with serrate margins, which is possibly the plesiomorphic condition for all Cunoniaceae genera. Within *Eucryphia* there has been an evolutionary trend towards simple leaves with entire margins and well developed peltiform cuticular extensions.

Introduction

Eucryphia Cav. is an interesting genus because there is still some debate about its exact taxonomic status. It has been placed near the Rosaceae (Bentham and Hooker 1862), in the

monotypic Eucryphiaceae (Focke 1895) or nested in a broad Cunoniaceae (Bausch 1938; Cronquist 1981; Thorne 1983; Takhtajan 1987; Hufford 1992). This latter assignment has been supported by phylogenetic analyses using morphological characters (Hufford 1992; Hufford and Dickison 1992), and *rbc*L gene (Chase *et al.* 1993; Morgan and Soltis 1993) and 18S rDNA sequences (Soltis *et al.* 1997). On this basis, *Eucryphia* is accepted herein to be a genus within a broad Cunoniaceae.

The examination of the fossil record of *Eucryphia* can provide a minimum age for its origin and possibly help to identify the form of the ancestor or ancestral complex to this genus and, more generally, the Cunoniaceae. This is particularly important when interpreting and scoring ancestral characters for any phylogenetic analyses. Currently, two species are recognised in South America (Holdgate 1961; Veblen and Schlegel 1982; Rancusi *et al.* 1987; Rodriguez *et al.* 1983; Zegers and Garcia 1994; Zegers 1995) and five in Australia (Boland *et al.* 1985; Read and Busby 1990; Hill 1991*a*; Forster and Hyland 1997; Fig. 1). Two subspecies have been recognised within the Tasmanian endemic *E. milliganii* Hook.f. (Barnes *et al.* in press).

The identification of *Eucryphia* leaf macrofossils has been well discussed by Hill (1991*a*). *Eucryphia* has a very extensive fossil record with macrofossils identified from 11 Cainozoic deposits in south-eastern Australian (Table 1). All described macrofossil species prior to this present study are represented by leaves or leaf fragments and possess simple unicellular trichome bases, stoma with a brachyparacytic subsidiary cell arrangement, and abaxial peltiform cuticular extensions to some extent (Hill 1991*a*), which form the basis of most identifications. The oldest fossil *Eucryphia* species, *E. falcata* R.S. Hill from Lake Bungarby (Late Palaeocene), has compound leaves consisting of possibly five leaflets. It probably resembles the ancestral leaf form of the genus, which is serrate and falcate (Taylor and Hill 1996). The Early Eocene Regatta Point species *E. microstoma* R.S. Hill has unusually small stomata (Hill 1991*a*) and may not even represent *Eucryphia* although at this stage the assignment is accepted here but remains tentative.

Macrofossils of *Eucryphia* from Early Pleistocene Regatta Point sediments have been extensively studied (Hill and Macphail 1985, Hill 1991*a*, Jordan 1992, Taylor 1993). Hill (1991*a*) assigned the fossils to *E.* aff. *milliganii* as they may equally represent leaves of *E. milliganii* or a form that immediately preceded that observed in *E. lucida*. Macrofossils conspecific to the two extant Tasmanian species *E. lucida* and *E. milliganii* have been located in the Middle Pleistocene Regency Formation (Fitzsimons *et al.* 1990; Jordan 1992; Taylor 1993) and those of *E. lucida* have been recovered from Late Pleistocene sediments at the Pieman Dam (Colhoun 1980), both in western Tasmania (see Fig. 1). Fossil *E. gregorii* Deane from Cainozoic sediments at Pitfield in Southern Victoria is unverified because the specimen could not be relocated and is only illustrated by a line drawing (see Deane 1902).

This study describes three new macrofossil species of *Eucryphia* from Tasmanian Cainozoic localities, including the first fossil capsule of two ever recorded. The macrofossils described by Hill (1991*a*) as *Eucryphia* are also re-examined, with particular emphasis on *E.*

aberensis from Loch Aber and *E.* aff. *milliganii* from the Early Pleistocene sediments at Regatta Point. The implications of these fossils on the diversity, evolution and possible ancestral form of the genus are also discussed.

Materials and Methods

Extant Specimens

Fresh and dried herbarium specimens of all extant species were available for this study. Leaves of *E. lucida* (Labill.) Baill., *E. moorei* F.Muell., *E. glutinosa* (Poepp. et Endl.) Baill., *E. cordifolia* Cav. and the two subspecies of *E. milliganii* Hook.f., *E. milliganii* ssp. *milliganii* and *E. milliganii* ssp. *pubescens* R.W.Barnes, G.J.Jord., R.S.Hill & C.J.McCoull (see Barnes *et al.* in press), were examined from the herbarium and living collection housed at the School of Plant Science, University of Tasmania. Leaves of *E. wilkiei* B.Hyland were collected from the only known population (17°24'30" S, 145°49' E; Fig. 1). Leaves of *E. jinksii* P.I.Forst. were collected from Natural Arch National Park, Springbrook (28°14' S, 153°13' E; Fig. 1) by P. I. Forster and preserved in 5:5:90 40% formalin-acetic acid-alcohol solution (FAA). Specimens examined covered the geographic range of each species.

The leaf cuticle was prepared by placing specimens in 10-50% aqueous hydrogen peroxide solution with several crystals of tetra-sodium pyrophosphate and warmed on a hot plate (30-35 °C) for 24 hours or until all other organic matter had oxidised. Prepared cuticles were rinsed in distilled water, stained in 1% aqueous safranin O, mounted in phenol glycerine jelly and observed with a Zeiss Axioskop microscope. For scanning electron microscopy, prepared cuticles or leaf fragments were placed onto aluminium stubs with double-sided carbon tape. Samples were sputter coated with gold to a thickness of 20 nm and examined with an Environmental Scanning Electron Microscope 2020 (ESEM) operated at 15-20 kV. Terminology of both fossil and extant species follows Hickey (1979) for leaf architecture and Dilcher (1974) for cuticular and stomatal morphology.

Fossil Localities and Specimens

All *Eucryphia* fossil localities, with the exception of Lake Bungarby, occur within Tasmania (Fig. 1; Table 1). Leven River macrofossils were extracted from a macerate prepared by soaking blocks of sediment in 10% hydrofluoric acid for 2-4 weeks then rinsing with water to dissociate the sediment and macrofossils. All macrofossils were photographed with a Canon EOS camera using a low angle light source. The cuticle of each fossil was prepared as for the extant species.

Lea River

This locality in north-western Tasmania has been palynostratigraphically aged as Early Oligocene (M. K. Macphail personal communication). The deposit contains abundant, well preserved mummified leaves, fruits, twigs and wood and included Proteaceae (Jordan *et al.* 1998), Cupressaceae (Hill *et al.* 1993; Hill and Whang 1996) and *Nothofagus* (Whang and Hill

1995; Scriven and Hill 1996) but also many undescribed taxa. A fossil capsule (Lea-3301) and a leaf fragment (Lea-3302) assignable to *Eucryphia* were extracted from macerated sediment.

Wilson's Creek

Fossils occur more or less in horizontally bedded siltstones and fine sandstones exposed for approximately 60 m along the bed and banks of Wilson's Creek at 42°19'10" S, 146°27'25" E at about 460 m above sea level (Jordan and Hill 1998). The sediments are overlain and underlain by basalts and range from scarcely to moderately lithified, possibly due to heating from cooling lava. Other lenses of similar sandstones are exposed upstream, and apparently stratigraphically above the fossiliferous lens. The sediments are ?Latest Eocene-Early Oligocene based on palynostratigraphic evidence (M. K. Macphail personal communication) which is supported by the presence of fossils of large-leaved *Nothofagus*, a range of imbricate conifers and a large diversity of extinct angiosperms. The overlying and underlying basalts have not been dated. A single compression fossil of a *Eucryphia* leaf (WC-33) was extracted and is described here.

Loch Aber

This locality in north-eastern Tasmania contains a diverse fossil flora including mummified leaves, leaf fragments, wood and reproductive structures, though only *Eucryphia aberensis* (Hill 1991*a*), *Banksieaephyllum attenuatum* Hill & Christophel (Hill and Christophel 1988), and six species of conifer (Hill 1989; Hill 1990; Hill and Carpenter 1991, Hill and Pole 1992) have been formally described from this deposit. The locality is Middle to Late Eocene in age based on palynostratigraphy (see Hill and Christophel 1988). The specimens of *E. aberensis* that were examined by Hill (1991*a*) were available for this study in addition to specimens from more recent collections of the locality. An emended diagnosis for *E. aberensis* is presented. Specimens have the prefix LA.

Little Rapid River

Macrofossils from this Early Oligocene deposit in north-western Tasmania (Macphail *et al.* 1994) have been described by several authors (e.g. Hill and Carpenter 1989; Hill and Scriven 1997; Barnes and Hill in press). Mummified leaves and reproductive structures are preserved in coarse sands and include *Nothofagus* subgenus *Brassospora* (Hill 1991*b*), Lauraceae, *Gymnostoma* (Hill and Scriven 1997) and a large diversity of conifers (see Hill 1995). Several leaf fragments and a capsule which are assignable to *Eucryphia* were examined during this study. Specimens have the prefix LRR1.

Regatta Point

Three fossiliferous deposits that contain *Eucryphia* macrofossils occur at Regatta Point in western Tasmania (see Jordan and Hill 1998). Underlying Early Eocene sediments are overlain by glacial outwash that contains clay clasts of Early Pleistocene and Early-Middle

Pleistocene age (Table 1). *Eucryphia microstoma* (Hill 1991*a*) has been described from the Early Eocene sediments. Dispersed cuticle of an unknown *Eucryphia* species has been recorded from the Early-Middle Pleistocene clasts (Jordan *et al.* 1995).

The Early Pleistocene clasts are primarily aged on palynostratigraphy (Macphail *et al.* 1993; Jordan and Hill 1994). The flora has been extensively studied (e.g. Hill and Macphail 1985; Macphail *et al.* 1993; Jordan 1992, 1995*a*, 1995*b*, 1997, in press) and included many extant Tasmanian rainforest species (see Hill and Macphail 1985; Jordan 1995*a*, 1995*b*). Despite its recent age, several genera present in the deposit are now extinct in Tasmania, including *Dacrycarpus* (Jordan 1995*b*) and *Quintinia* (Macphail and Hill 1985; Jordan 1997). Mummified leaves and leaf fragments of *Eucryphia* are abundant in the deposit and have been studied by Hill and Macphail (1985), Hill (1991*a*), Jordan (1992), Taylor (1993) and Taylor and Hill (1996). These were re-examined during this study. Specimens have the prefix RPU.

Regency Formation

The Regency Formation occurs in western Tasmania. Fitzsimons *et al.* (1990) argued that it is Early-Middle Pleistocene in age but E. A. Colhoun (personal communication) and Jordan and Hill (1994) considered that the age is more likely to be Middle Pleistocene based on sedimentological and palaeofloristic grounds. Macrofossils of *Eucryphia* have been extracted and studied by Fitzsimons *et al.* (1990), Jordan (1992) and Taylor (1993). These were re-examined during this study.

Leven River

Based on palynostratigraphy, this locality in north-western Tasmania is Early Oligocene in age (Carpenter and Jordan 1997; Jordan *et al.* 1998) and contains mummified leaves and wood. A single species of Proteaceae, *Orites excelsoides* R.J.Carp. & G.J.Jord., has been described from the deposit which also contains *Nothofagus, Eucryphia*, other angiosperms and at least four imbricate leaved conifer species (Carpenter and Jordan 1997).

Results

Lea River

The fossil capsule shares many features with those of extant *Eucryphia* species, including the large number and shape of the valves, their dehiscence and attached apical style. Extant *Eucryphia* capsules are composed of 5-14 (-18) boat-shaped valves each with a terminal style (Bausch 1938; Dickison 1978; Harden 1990; Fig. 2) that dehisce septicidally (Harden 1990), with a vascular connective fused to the inner endocarp for the length of the valve (Fig. 3). This connective splits near the valve suture and continues to the apical style, along the inner edge of the endocarp (Dickison 1978; Fig. 3). The endocarp and exocarp are fused but remain distinct (see Fig. 3). The endocarp is thin and papery while the exocarp is strongly lignified. At fruit maturity the receptacle retains the scars where the sepals were attached and the insertion point of the petals, immediately adjacent to the sepal scars (Fig. 4). The exocarp is covered in

simple trichome bases (Fig. 5) which vary in density among the extant species (see also Forster and Hyland 1997). The presence of a central vascular connective between the carpels for at least part the length of the capsule and persistent apical styles upon capsule maturity are also features in other Cunoniaceae, such as *Geissois* (Fig. 6), *Lamanonia, Ackama* and *Spiraeopsis* (see also Godley 1983), however *Eucryphia* is unique in the large number of valves per capsule.

The fossil *Eucryphia* capsule is complete with all eight valves still attached (Figs 7 and 8). Scars where the sepals were attached and probable petal insertion point are preserved on the receptacle at the base of the capsule (Fig. 9). The endocarp and exocarp are distinct, with the endocarp being thin and glabrous (Fig. 10) while the exocarp is thicker, probably lignified and is covered in small trichome bases similar to those present on the exocarp of extant species, for example *E. lucida* (Fig. 10 cf. Fig. 5). The remnants of a vascular connective fused to the inner endocarp is preserved which splits at the valve suture, and is identical to the type of capsule dehiscence in the extant species (Fig. 12 cf. Fig. 3). Some valves contained well preserved seed coats which have a highly reticulate and indented surface, similar to the reticulate seed coat of extant *Eucryphia* species (Fig. 13 cf. Figs 14 and 15). A reticulate seed coat is also present in other Cunoniaceae, such as *Geissois* and *Lamanonia* (Dickison 1984; Hufford and Dickison 1992).

The fossil capsule has more valves than extant *E. milliganii* (4-5), *E. lucida* (5-7) and *E. moorei* (5-7) and is larger in size than the capsules of *E. wilkiei* and *E. jinksii*, which both have capsules of 7-9 valves. The capsule is most similar to those present in the two South American species *E. glutinosa* and *E. cordifolia* based on size and the number of valves but the seed coat of the fossil is more strongly reticulate and deeply indented than any living species. The fossil capsule could be conspecific with the fossil leaf species described from this or another deposit but in the absence of any organic connection to a leaf or leaf fragment it is assigned to a new species, *Eucryphia reticulata.*

The single leaf fragment extracted from this locality (Lea-3302) is interpreted to be a leaflet derived from a compound leaf as it is highly falcate, especially in the upper section (Fig. 16). The leaflet has a cuneate base and entire margin. The apex is not preserved in its entirety but was probably acute in shape. It is not possible to determine if the species was polymorphic for leaf margin form as only a single leaflet is preserved. Secondary venation is brochidodromous with only few lateral vein pairs. Stoma have a brachyparacytic subsidiary cell arrangement (Fig. 17) and occur in weak areoles (Fig. 18). The abaxial lamina has well developed peltiform extensions (Figs 17 and 18) that also extend onto the minor veins (Figs 19 and 20) but are absent from the entire length of the midrib (Fig. 21). Unicellular trichome bases are present on the minor veins and midrib (Figs 20 and 21) and are surrounded by 5-6 epidermal cells with a slight thickening of the inner surface (e.g. Fig. 20). The leaf margin is sparsely pubescent (Fig. 22). The epidermal cells on the adaxial surface are isodiametric and there are numerous trichome bases preserved (Fig. 23).

On the basis that the leaflet is from a compound leaf, and that the margin is entire, it is most similar to the fossil taxon *E. aberensis* and the three extant species *E. moorei, E. wilkiei* and *E. jinksii*. However, the fossil leaf differs from these species as it has a pubescent abaxial lamina (nearly glabrous in *E. aberensis*) and sparsely pubescent margins (numerous hairs in *E. moorei, E. wilkiei* and *E. jinksii*). Although these features distinguish it from these taxa it may be derived from the same parent plant as *E. reticulata*, but in the absence of an organic connection it is assigned to a new species, *Eucryphia leaensis.*

Wilson's Creek

The specimen WC-33 (Fig. 24) is the only fossil *Eucryphia* leaf extracted from Wilson's Creek. The leaf is incomplete, approximately 70 mm long and 26 mm wide at the widest point without the apex preserved (Fig. 24). The base is acute and symmetrical, so it is not possible to determine if it is a simple leaf, or a terminal leaflet, or a symmetrical lateral leaflet. The margin is irregularly serrate with a prominent, apically directed mucronate extension on each tooth apex (Fig. 24), similar to those in extant *E. glutinosa.*

Stomata are restricted to the abaxial surface and have a brachyparacytic subsidiary cell arrangement (Fig. 25). Peltiform extensions are well developed on the abaxial lamina (Figs 26 and 27), poorly developed on minor veins (Fig. 27) and are entirely absent from the midrib (Fig. 28). Grooves lead in to the cuticular extensions (Fig. 29). Trichome bases are simple, surrounded by 5-7 radially arranged epidermal cells (Fig. 30) and are restricted to the midrib and higher veins on both surfaces. Hydathodes are also present on the major abaxial veins (Fig. 31) and the midrib.

The fossil taxon described here has several features characteristic of evergreen *Eucryphia* species and include a brachyparacytic subsidiary cell arrangement (Fig. 25), dense abaxial peltiform extensions (Figs 26 and 27) and simple unicellular trichome bases with radially arranged slightly modified epidermal cells (Fig. 30) on both leaf surfaces. Like the leaves of the two South American species, *E. cordifolia* and *E. glutinosa*, and the juvenile leaves of *E. moorei, E. lucida* and *E. milliganii*, the fossils' margins have several irregular mucronate teeth. However, the fossil differs from *E. glutinosa* by the presence of well developed cuticular peltiform extensions and from *E. cordifolia* by the presence of an acute leaf base. The fossil is most similar to the fossil taxa *E. falcata* from Lake Bungarby and *E. aberensis* from Loch Aber but differs in having well developed abaxial peltiform extensions (unlike *E. falcata*) and trichomes on the abaxial lamina (unlike *E. aberensis*) so it is assigned to a new species, *Eucryphia mucronata.*

Loch Aber

Numerous leaves and leaf fragments of *E. aberensis* were extracted from Loch Aber sediment and examined in conjunction with those from the study of Hill (1991*a*). Hill (1991*a*) suggested that the macrofossils of *E. aberensis* may represent single leaves or leaflets from a compound leaf. The latter hypothesis is supported by both the discovery of two *Eucryphia*

leaflets with an organic connection preserved (Figs 32 and 33) and the presence of leaflets with either an asymmetrical (Fig. 34) or symmetrical leaf base (Fig. 35). The leaflets either have entire margins (Figs 35 and 36) and brochidodromous venation (Fig. 36) or are serrate, at least in the apical region (Fig. 37). A single leaflet apex was located and is attenuate in shape (Fig. 38). The variation in leaf form may be interpreted as representing two *Eucryphia* species. However, it is more probable that *E. aberensis* was polymorphic for leaf margin form given that all leaflets examined possessed well developed peltiform cuticular extensions (Figs 39 and 40), a brachyparacytic subsidiary cell arrangement (Fig. 39), a glabrous abaxial lamina (Figs 39 and 40) and sparse unicellular trichome bases on the midrib (Fig. 41) and margins (Fig. 42).

Peltiform cuticular extension development and trichome distribution in *E. aberensis* is similar to that observed in extant *E. lucida* and *E. milliganii* ssp. *milliganii*, however these species have leaves with entire margins and are predominantly simple. The shape and size of the serrations in *E. aberensis* are similar to those in *E. mucronata* (Fig. 37 cf. Fig. 24) but differs from this species, and all other fossil leaf species, in possessing a glabrous abaxial lamina. Therefore, the specific status of *E. aberensis* is supported. An emended diagnosis is presented here to include the presence of compound leaves consisting of leaflets with entire or serrate margins.

Little Rapid River

The leaf fragments examined from this locality are consistent with having been part of a compound leaf as the leaf bases are either symmetrical (Fig. 43) or asymmetrical (Fig. 44). Leaflets either have an entire margin (Figs 45 and 46) or are serrate, at least in the apical region (Figs 47 and 48), with tooth apices similar in shape to those of *E. aberensis* from Loch Aber (cf. Fig. 29). As with *E. aberensis* from Loch Aber, the variation in leaf margin form is interpreted here as being consistent with variation within a single species, especially since the cuticle morphology of all the specimens examined is identical. In particular, all leaflets possess a brachyparacytic subsidiary cell arrangement (Fig. 49) and well developed peltiform cuticular extensions (Fig. 50) that occur on minor veins (Fig. 51) but are absent from the midrib (Fig. 50). Simple unicellular trichome bases occur on the abaxial midrib (Fig. 50) but are absent from the abaxial lamina and veins (Fig. 51). Marginal trichome bases are sparse (Fig. 52) and the adaxial surface is glabrous (Fig. 53). On the basis of leaflet shape and form, and foliar hair distribution, the fossils differ from all extant and fossil taxa except for *E. aberensis* so are assigned to that species here.

The fossil capsule extracted from this locality is not complete. The capsule is poorly preserved as two attached valves, with the remnants of a terminal style on a single valve only (Figs 54-56). One valve is prominently keeled (Fig. 56). It is not possible to determine the exact number of valves that would have formed the capsule, but it would have been more than six based on the dimensions of the preserved valves. This excludes all other Cunoniaceae genera with dehiscent capsules as these all possess two or three valves (e.g. Dickison 1984; Hufford and Dickison 1992). The receptacle, which was preserved in *E. reticulata* (Fig. 9), is

absent from this specimen but the valves do possess a distinct endo- and exocarp (Figs 54 and 55) and the remnants of a vascular connective fused to the inner endocarp (Fig. 57), similar to that in extant *E. lucida* (cf. Fig. 3) and fossil *E. reticulata* (cf. Fig. 12). Occasional unicellular trichome bases are present on the exocarp (Fig. 59) which are similar to those in extant *E. lucida* (cf. Fig. 5) and extinct *E. reticulata* (cf. Fig. 11). No seed coats were located in the dehisced valves.

The incomplete capsule has features characteristic of *Eucryphia* (multiple boat-shaped valves, terminal apical style, vascular connective fused to the inner endocarp and a distinct endocarp and exocarp that is pubescent) but because the number of valves is unknown the specimen cannot be assigned with confidence to either an extant or extinct genus. It is possible that the capsule is conspecific with *E. aberensis,* which is represented by leaves in both this and the Loch Aber deposit, but cannot be confirmed due to the lack of any organic connection. As additional specimens need to be located and examined to determine the affinities of the fossil capsule it will be referred to as *Eucryphia* sp. 'LRR1'.

Regatta Point

The Early Pleistocene *Eucryphia* macrofossils from Regatta Point have received appreciable attention, particularly from Hill (1991*a*), Taylor (1993) and Taylor and Hill (1996). The fossils examined by Hill (1991*a*) had a glabrous abaxial surface except for a few scattered hairs along the midrib. This pattern was considered by Hill (1991*a*) to be at one end of the variability in *E. milliganii* and is identical to that present in *E. lucida* so the fossils were assigned to *E.* aff. *milliganii.* This identification was accepted by Taylor and Hill (1996) in a phylogenetic study of the fossil species described at that time.

A re-examination of the *Eucryphia* macrofossils extracted during previous studies (e.g. Jordan 1992) indicated that the fossil leaves fall into two distinct groups based on differences in foliar hair distribution and density. In particular, all macrofossils are identical in foliar hair distribution and density to that observed within either extant *E. lucida* (Hill 1991*a*; Taylor 1993; Taylor and Hill 1996) or the subspecies of *E. milliganii* (Barnes *et al.* in press). *Eucryphia lucida* has a glabrous abaxial surface with dense hairs along the leaf margins (Hill 1991*a*; Taylor 1993). Barnes *et al.* (in press) have shown that there are two subspecies of *E. milliganii* based on leaf shape and leaf pubescence. *Eucryphia milliganii* ssp. *milliganii* has oblong leaves with a glabrous abaxial surface and sparse trichomes along the margins while leaves of *E. milliganii* ssp. *pubescens* are ovate to elliptic with a pubescent abaxial lamina and margins.

Numerous whole and fragmented large (Figs 60-63) and small leaves (Figs 64-67) of fossil *E. lucida* were identified. Leaf bases are symmetrical (e.g. Figs 61 and 63) and therefore probably represent simple leaves. However, even in trifoliate leaves of extant *E. lucida* it is very difficult to differentiate between lateral and terminal leaflets. The single leaf with apical serrations (Fig. 67) probably represents a juvenile leaf as rosid teeth are common in the first few leaves of seedlings (Hill 1991*a*) and occasionally on coppice growth (R.W. Barnes pers. obs.). The abaxial cuticle in all cases is glabrous (Fig. 68), with the exception of a few

trichome bases along the midrib, and the margins preserve densely arranged trichome bases (Fig. 69). The leaves described here conform to the pattern of foliar hair distribution in extant *E. lucida* and, although variable in size, occur within the size range of the extant species, so are assigned to *E. lucida* here.

The fossils leaves and leaf fragments of *E. milliganii* ssp. *milliganii* (Figs 70-74) are smaller and less common than those of *E. lucida*. Leaves are linear to oblong in shape and have an emarginate apex (Figs 70 and 71). The abaxial cuticle is glabrous (Fig. 75), with scarce to no trichome bases on the leaf margin (Fig. 76). On the basis of leaf shape, a glabrous abaxial lamina and sparsely pubescent margins the leaves are assigned to the extant species *E. milliganii* ssp. *milliganii* here.

Regency Formation

The macrofossils of *Eucryphia* from the Regency Formation are conspecific with the two extant Tasmanian species *E. lucida* and *E. milliganii* on the basis of leaf shape and foliar hair distribution, which is in accordance with Fitzsimons *et al.* (1990), Jordan (1992) and Taylor (1993). More specifically, the majority of the leaf macrofossils are typical of *E. milliganii* ssp. *milliganii* as they are oblong to elliptic in shape and have a glabrous abaxial lamina and nearly glabrous margins (see Taylor 1993).

Leven River

Some fragments of dispersed cuticle located in the Leven River sediment are typical of *Eucryphia* (abaxial peltiform extensions, a brachyparacytic subsidiary cell arrangement and simple unicellular trichome bases); however, no whole or fragmented macrofossils were located. This cuticle could not be distinguished from most evergreen extant or fossil species. The presence of well developed peltiform extensions, a groove leading into the epidermal cells and trichome bases restricted to the midrib suggests an affinity to the extant Australian species *E. lucida* and *E. milliganii* ssp. *milliganii* and the fossil taxon *E. aberensis*. As leaves or leaf fragments need to be examined to enable an identification at the species level the cuticle will be referred to as *Eucryphia* sp. 'Leven'.

Systematics

Family: Cunoniaceae R.Br.

Eucryphia Cav.

Eucryphia reticulata R.W.Barnes & G.J.Jord., sp. nov. (Figs 7-13)

Diagnosis

Eight valved, septicidally dehiscent capsule. Sparsely pubescent exocarp, hair bases simple, unicellular. Seed coats strongly reticulate and deeply indented.

Holotype: Lea-3301 (single specimen), stored in the School of Plant Science, University of Tasmania.

Type locality

Early Oligocene sediments at Lea River, north-western Tasmania.

Etymology

Named in recognition of the strongly reticulate and deeply indented seed coat.

Eucryphia leaensis R.W.Barnes & G.J.Jord., sp. nov. (Figs 16-23)

Diagnosis

Leaf compound. Leaflet margin entire, sparsely pubescent. Well developed abaxial peltiform cuticular extensions. Abaxial midrib and veins pubescent.

Holotype: Lea-3302 (single specimen), stored in the School of Plant Science, University of Tasmania.

Type locality

Early Oligocene sediments at Lea River, north-western Tasmania.

Etymology

Named after the Lea River locality.

Eucryphia mucronata R.W.Barnes & G.J.Jord., sp. nov. (Figs 24-31)

Diagnosis

Leaf, base acute. Margins irregularly serrate, tooth apices distinctly mucronate. Well developed abaxial peltiform cuticular extensions. Abaxial lamina, midrib and margins pubescent, hair bases simple, unicellular.

Holotype: WC-33 (single specimen), stored in the School of Plant Science, University of Tasmania.

Type locality

Early Oligocene sediments at Wilson's Creek, near Tarraleah, central Tasmania.

Etymology

Highlights the mucronate tooth apices the length of the leaf.

Eucryphia aberensis R.S.Hill p. 491, figs 31-38. (Figs 32-53)

Emended diagnosis

Leaf compound, leaflets with serrate or entire margins and an attenuate apex. Well developed abaxial peltiform cuticular extensions.

Holotype: LA-013 (housed in the Department of Environmental Biology, University of Adelaide).

Specimens Examined

LA-009, 013, 018, 029, 048, 212, 220, 222, 223-229, 235-236, 238-247.
LRR1-4010, 4011, 4013-4014, 4016-4017, 4019-4020, 4022-4028, 4030-4045, 4047-4052, 4057.

Type locality

Middle to Late Eocene sediments at Loch Aber, north-eastern Tasmania.

Discussion

Fossil Species

The *Eucryphia* macrofossil record is represented by leaves, leaf fragments and two capsules (Table 1). *Eucryphia reticulata* (Lea River; Early Oligocene) is the first fossil capsule of *Eucryphia* to be described and has similarities to the extant South American species, *E. glutinosa* and *E. cordifolia* based on the number of valves and overall size. The capsule occurs with a single leaf macrofossil, *E. leaensis*, that probably represents a leaflet from a compound leaf based on its highly falcate shape. The leaflet has an entire margin and may be conspecific with *E. reticulata* but requires an organic connection to confirm this.

The second capsule, *Eucryphia* sp. 'LRR1', is incomplete and is generally too poorly preserved to be assigned to an extinct or extant species. This capsule may be conspecific with *E. aberensis*, with which it occurs (Little Rapid River), but again this cannot be confirmed because of the lack of an organic connection. *Eucryphia aberensis* is the first fossil *Eucryphia* species to be recorded from more than one locality and has compound leaves formed by serrate and entire margin leaflets. The species had evolved prior to the Middle to Late Eocene (Loch Aber) and persisted until at least the Early Oligocene (Little Rapid River). *Eucryphia mucronata* from Wilson's Creek has irregularly serrate margins and may represent a simple leaf, terminal leaflet or a symmetrical lateral leaflet of a compound leaf. The *Eucryphia* macrofossils from Regatta Point (Early Pleistocene) and the Regency Formation (Middle Pleistocene) are conspecific with the extant Tasmanian species *E. lucida* and *E. milliganii* ssp. *milliganii.*

The oldest fossil *Eucryphia* species, *E. falcata* from Lake Bungarby, has compound leaves with serrate margins which probably resembles the ancestral form of the genus (see also Taylor and Hill 1996). The assignment of *E. microstoma* from Regatta Point (Early Eocene) to the genus is doubtful, however as no alternative generic placement has been identified, the fossil will remain in the genus. This latter species will not be considered in the examination of the evolutionary trends within the genus.

Evolutionary Trends in Eucryphia

The revised fossil record of *Eucryphia* indicates that there have been three, probably unrelated, evolutionary trends in leaf morphology; the development of entire leaf/leaflet margins, the development of peltiform cuticular extensions on the abaxial lamina, and leaf simplification (Fig. 77). As suggested by Taylor and Hill (1996), the ancestral form in *Eucryphia* probably had compound leaves with serrate margined leaflets (Fig. 77), with leaf form evolving in response to climatic changes during the Cainozoic (e.g. decreasing temperatures and precipitation and increasing seasonality; Quilty 1994). Leaf evolution in response to climate change has also been suggested for other lineages with extensive fossil records in south-eastern Australia, such as *Nothofagus* (Hill 1991*b*, 1994), Casuarinaceae (Hill 1994) and *Acmopyle* and *Dacrycarpus* (Hill and Carpenter 1991; Hill 1994).

Eucryphia aberensis from Loch Aber shows that entire leaf margins had evolved by the Late Eocene. The variability in leaf form present in *E. aberensis* does not occur in any extant species as all extant species have adult leaves with entire margins except for *E. glutinosa* and *E. cordifolia*. Entire margins are the derived condition in the extant Australian species, although their origin may be polyphyletic based on the cladogram of Taylor and Hill (1996) that included the extant and extinct taxa at that time. *Eucryphia moorei, E. lucida* and *E. milliganii* at least exhibit small rosid teeth in the juvenile foliage (Boland *et al.* 1985; Hill 1991*a*) which supports a link to the ancestral form.

This fossil evidence suggests that the evolution of entire leaf margins postdates, and is independent of, the origin and development of peltiform cuticular extensions (Fig. 77). The extensions are poorly developed in *E. falcata* (serrate) but are well developed in *E. mucronata* (serrate), *E. aberensis* (serrate/entire), *E. leaensis* (entire) and the conspecific *E. lucida* (entire) and *E. milliganii* ssp. *milliganii* (entire) macrofossils from Regatta Point and the Regency Formation. Although their full ecological significance is unclear, Hill (1991*a*) and Taylor and Hill (1996) hypothesised that the extensions present in evergreen species may reduce transpirational water loss and/or increase frost resistance. The absence of extensions in *E. glutinosa* may be, in part, due to the species' deciduous habit. There may be fossils of deciduous *Eucryphia* but they are unrecognisable without the peltiform extensions.

Peltiform extensions were poorly developed in the Late Paleocene (*E. falcata*) but were well developed by the Middle to Late Eocene-Early Oligocene (*E. aberensis, E. leaensis* and *E. mucronata*) at the latest (Fig. 77). Since most authorities consider that the Early Tertiary was very wet (e.g. Truswell 1993; Hill 1994; Macphail *et al.* 1994; Quilty 1994) it is very doubtful

that the peltiform cuticular extensions initially evolved as an adaptation to reduce water loss. In particular, the oldest fossil record is at Lake Bungarby (*E. falcata*) which is likely to have been a wet environment (Taylor *et al.* 990). Furthermore, the modern relatives of other fossil taxa that co-occurred with the extinct *Eucryphia* species are not generally associated with dry climates (e.g. Hill 1994, 1995) and is further supported by the restriction of extant species to everwet cool temperate habitats from sea level to the subalpine zone and at higher altitudes in the subtropical and warm temperate zone where water would be rarely if ever limiting. However, it is plausible that the enhanced development of the peltiform extensions through the Cainozoic was, at least in part, due to increasing cold, frost, seasonality or some combination of these.

A reduction in the number of leaflets within a compound leaf clearly post-dates the evolution of peltiform cuticular extensions and entire margins. Similar trends in the reduction in leaflet number has been suggested by Hufford and Dickison (1992) within several other Cunoniaceae genera.

A revised phylogeny including all extant and extinct species may further elucidate the evolutionary relationships within the genus.

Acknowledgments

We thank Professor Robert Hill for his support and critical comments, and Carlos Lehnebach (Universidad Austral de Chile) for specimens of South American *Eucryphia* species. Scanning electron microscopy facilities were provided through the Central Science Laboratories, University of Tasmania (Dr. David Steele). This work formed part of the first author's Ph.D. funded through an Australian Postgraduate Award.

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Fig. 1. Past and present distribution of *Eucryphia* in eastern mainland Australia and Tasmania (inset). Fossil localities of the genus are shown as squares. The distribution of widespread species are shaded, those of restricted species are shown as circles. The subspecies of *E. milliganii* differ in their distribution in Tasmania; *E. milliganii* ssp. *milliganii* occurs in the north-west and west while *E. milliganii* ssp. *pubescens* occurs in the south and south-west. *Eucryphia lucida* occurs throughout the range of both *E. milliganii* subspecies. The Regatta Point locality has Early Eocene and overlying Early Pleistocene and Early-Middle Pleistocene sediments. Geological ages for localities are listed in Table 1.

Figs 2-5. Capsule features of *Eucryphia lucida*. **Fig. 2.** Whole capsule. Scale bar = 10 mm. **Fig. 3.** Partially dissected capsule showing the thin vascular connective fused to the inner endocarp. Note the splitting of the connective near the valve suture (arrow). Scale bar = 10 mm. **Fig. 4.** Scanning electron micrograph of the receptacle showing the pedicel (Pd), a prominent scar from a detached sepal (S) and petal insertion point (P). Scale bar = 500 μm. **Fig. 5.** Unicellular trichome base on exocarp. Scale bar = 25 μm.

Fig. 6. Dehisced capsule of *Geissois biagiana* showing terminal styles that split at fruit maturity (black arrow) and central vascular connective between the dehisced carpels (white arrow). Scale bar = 10 mm.

Figs 7, 9-13. Holotype of *Eucryphia reticulata* R.W.Barnes & G.J.Jord., sp. nov. (Lea-3301) from Lea River, north-western Tasmania.

Fig. 7. Macrofossil with remnants of terminal style (arrow). Scale bar = 10 mm.

Figs 9-13. Scanning electron micrographs. **Fig. 9.** Receptacle showing two prominent sepal scars (S) and adjacent petal insertion point. Scale bar = 500 μm.

Fig. 10. Side view of valve showing glabrous endocarp (En) and distinct exocarp (Ex). Scale bar = 200 μm. **Fig. 11.** Unicellular trichome base on exocarp. Scale bar = 25 μm.

Fig. 12. Side view of valve showing vascular connective (Vc) fused to the inner endocarp and connective bifurcation (B) near the valve suture (top right). Scale bar = 400 μm.

Fig. 13. Seed coats dissected from within the valves. Scale bar = 200 μm.

Figs 14, 15. Scanning electron micrographs of the seed coat of extant *Eucryphia* species. **Fig. 14.** *E. lucida*. Scale bar = 50 μm. **Fig. 15.** *E. cordifolia*. Scale bar = 200 μm.

Fig. 8. Holotype of *Eucryphia reticulata* R.W.Barnes & G.J.Jord., sp. nov. (Lea-3301; Fig. 7) from Lea River. Note the attached receptacle and the single terminal style preserved on a single valve. Scale bar = 5 mm.

Figs 16-23. Holotype of *Eucryphia leaensis* R.W.Barnes & G.J.Jord., sp. nov. (Lea-3302) from Lea River, north-western Tasmania. **Fig. 16.** Macrofossil. Note the highly falcate leaf shape. Scale bar = 5 mm.

Figs 17-22. Light micrographs of the abaxial cuticle. **Fig. 17.** Stoma (centre) showing a brachyparacytic subsidiary cell arrangement (arrows indicate the positions of subsidiary cells). Scale bar = 30 μm. **Fig. 18.** Stomata occur in weak areoles and are obscured by well developed peltiform extensions. Scale bar = 100 μm. **Fig. 19.** Epidermal cells on a minor vein showing peltiform extensions (arrow). Scale bar = 50 μm. **Fig. 20.** Unicellular trichome bases on a minor vein (arrows). Scale bar = 80 μm. **Fig. 21.** Apical midrib showing unicellular trichome bases (arrows) and a lack of peltiform extensions. Scale bar = 100 μm. **Fig. 22.** Leaf margin showing sparse trichome bases (arrow). Scale bar = 250 μm. **Fig. 23.** Light micrograph of the adaxial cuticle showing isodiametric epidermal cells and unicellular trichome bases (arrows). Scale bar = 70 μm.

Figs 24-31. Holotype of *Eucryphia mucronata* R.W.Barnes & G.J.Jord., sp. nov. (WC-33) from Wilson's Creek.

Fig. 24. Macrofossil showing mucronate tooth apices (arrows). Scale bar = 10 mm.

Figs 25-31. Light and scanning electron micrographs of the abaxial cuticle of WC-33.

Fig. 25. Inner surface of a stoma showing brachyparacytic subsidiary cell arrangement (arrows indicate the positions of subsidiary cells). Scale bar = 25 μm.

Figs 26-28. Outer surface showing the distribution of cuticular peltiform extensions.

Fig. 26. Well developed lamina extensions. **Fig. 27.** Vein (arrow) showing weak extension development. Scale bar for both = 50 μm. **Fig. 28.** Apical midrib with no extensions. Scale bar = 150 μm.

Fig. 29. Inner surface showing groove in epidermal cell (arrow). Scale bar = 40 μm. **Fig. 30.** Unicellular trichome base on midrib with radially modified epidermal cells. Scale bar = 50 μm. **Fig. 31.** Hydathode on vein. Scale bar = 30 μm.

Figs 32, 34-42. *Eucryphia aberensis* from Loch Aber, north-eastern Tasmania.
Fig. 32. Incomplete compound leaf (LA-222) with leaflets still attached (arrow).
Fig. 34. Probable leaflet (LA-239) with asymmetrical base (arrow). **Fig. 35.** Entire margin leaf or leaflet (LA-245) with symmetrical base. **Fig. 36.** LA-245 showing brochidodromous secondary venation. **Fig. 37.** LA-229 showing apical serrations (arrows). Scale bars for Figs 26-29 = 10 mm. **Fig. 38.** Attenuate apex (LA-227). Scale bar = 1 mm.
Figs 39-42. Light micrographs of the abaxial cuticle. **Fig. 39.** LA-222 showing stoma with brachyparacytic subsidiary cell arrangement (arrows indicate subsidiary cells) and well developed peltiform extensions. Scale bar = 100 μm. **Fig. 40.** Secondary vein of LA-212 showing well developed peltiform extensions (arrow). Scale bar = 100 μm. **Fig. 41.** Apical region of midrib of (LA-227) showing trichome bases and no peltiform extensions. Scale bar = 250 μm. **Fig. 42.** Sparse unicellular trichome bases (arrow) on leaf margin (LA-235). Scale bar = 60 μm.

Fig. 33. Line drawing of specimen LA-222 (*Eucryphia aberensis*; Fig. 32) from Loch Aber sediments. Note that the specimen represents a compound leaf formed by two leaflets (L) attached at the base (arrow). Scale bar = 10 mm.

Figs 43-53. *Eucryphia aberensis* from Little Rapid River, north-western Tasmania.
Fig. 43. Leaf or leaflet with symmetrical base (LRR1-4057). **Fig. 44.** Leaflet with asymmetrical base (LRR1-4010). Scale bar for both = 5 mm.
Figs 45, 46. Leaflets with entire margins. **Fig. 45.** LRR1-4024. **Fig. 46.** LRR1-4030. Scale bar for both = 5 mm.
Figs 47, 48. Leaflets with serrations (arrows). **Fig. 47.** LRR1-4027. Scale bar = 1 mm. **Fig. 48.** LRR1-4053. Scale bar = 5 mm.
Figs 49-51. Scanning electron micrographs of the abaxial cuticle (LRR1-4010).
Fig. 49. Inner surface of stoma showing brachyparacytic subsidiary cell arrangement (arrows). Scale bar = 20 μm. **Fig. 50.** Outer surface showing sparse unicellular trichome bases on midrib (arrow) and well developed peltiform extensions on lamina. Scale bar = 200 μm. **Fig. 51.** Minor vein (arrow) showing the presence of peltiform extensions. Scale bar = 200 μm.
Figs 52, 53. Light micrographs of the cuticle (LRR1-4010). **Fig. 52.** Sparse unicellular trichome bases (arrow) on leaf margin. Scale bar = 100 μm. **Fig. 53.** Adaxial cuticle. Scale bar = 250 μm.

Figs 54-59. Incomplete fossil capsule of *Eucryphia* sp. 'LRR1' (LRR1-4046) from Little Rapid River, north-western Tasmania.

Fig. 54. Macrofossil in side view. Note the single remnant apical style (black arrow) and the distinction between the exocarp and endocarp (white arrow). **Fig. 55.** Line drawing of the incomplete capsule in figure 46 showing the two attached valves, one with a remnant terminal style. The exocarp and endocarp are clearly distinct and a ventral suture is present on one valve. **Fig. 56.** Macrofossil showing the outer exocarp of each valve. Note the remnant terminal style (lack arrow) and a prominent keel (white arrow) on a single valve. Scale bar for Figs 46-48 = 5 mm.

Figs 57-59. Scanning electron micrographs the endocarp and exocarp. **Fig. 57.** Side view of a valve showing the remnants of a central vascular connective (arrow) fused to the inner valve. Scale bar = 100 μm. **Fig. 58.** Outer exocarp showing relatively glabrous surface with well preserved cellular outline. Scale bar = 200 μm. **Fig. 59.** Unicellular trichome base on exocarp (arrow). Scale bar = 20 μm.

Figs 60-76. Fossil *Eucryphia lucida* and *E. milliganii* ssp. *milliganii* leaves and abaxial cuticle from Early Pleistocene sediments at Regatta Point, western Tasmania.
Figs 60-67. *Eucryphia lucida* macrofossils. **Fig. 60.** RPU-4670. **Fig. 61.** RPU-4650. Scale bar for Figs 52, 53 = 10 mm. **Fig. 62.** RPU-4657. **Fig. 63.** RPU-4673. Scale bars for Figs 54, 55 = 10 mm. **Fig. 64.** RPU-4686. **Fig. 65.** RPU-4718. **Fig. 66.** RPU-4687. **Fig. 67.** RPU-4666. Note apical serrations. Scale bar for Figs 56-59 = 10 mm.
Figs 68, 69. Light micrographs of the abaxial cuticle of *Eucryphia lucida* (RPU-4650). **Fig. 68.** Abaxial surface showing glabrous midrib (arrow) and lamina. **Fig. 69.** Leaf margin showing densely arranged trichome bases (arrow). Scale bar for both = 200 μm.
Figs 70-74. *Eucryphia milliganii* ssp. *milliganii* macrofossils. **Fig. 70.** RPU-4660. **Fig. 71.** RPU-4655. **Fig. 72.** RPU-4653. **Fig. 73.** RPU-4707. **Fig. 74.** RPU-4698. Scale bar for Figs 62-66 = 10 mm.
Figs 75, 76. Light micrographs of the abaxial cuticle of *Eucryphia milliganii* ssp. *milliganii* (RPU-4655). **Fig. 75.** Abaxial surface showing glabrous midrib (left), lamina and vein (arrow). Scale bar = 300 μm. **Fig. 76.** Leaf margin showing a single trichome base (arrow). Scale bar = 200 μm.

Fig. 77. Stratigraphic distribution of selected fossil *Eucryphia* spp. in south-eastern Australia. The line to the left of each macrofossil indicates the stratigraphic age of the deposit in which it occurs. The oldest species, *E. falcata* and *E. aberensis*, had compound leaves with serrate margins. Leaves of *E. leaensis* were probably compound while those of *E. mucronata* were probably simple. The simple leaves of *E. milliganii* ssp. *milliganii* and *E. lucida* are illustrated from Regatta Point (Early Pleistocene) and are also indicative of those from the Regency Formation (Middle Pleistocene). Peltiform extension development on the abaxial lamina and midrib is shown (far right). These structures were present by the Early Paleocene, and were well developed by the Middle to Late Eocene (*E. aberensis*), but possibly earlier as there is a gap in the fossil record with the exclusion of *E. microstoma* (see text for explanation). The possible form of the ancestor to *Eucryphia* (compound leaves; serrate leaflet margins; no peltiform extensions) is also illustrated.

Table 1. Accepted records of *Eucryphia* macrofossils from south-eastern Australia

Three separate fossiliferous deposits occur at Regatta Point; Early Eocene [A] sediments overlain by glacial outwash that contains clay clasts of Early Pleistocene [C] and Early-Middle Pleistocene [B] age.

Taxon	Fossil locality	Macrofossil	Geological age
Eucryphia falcata [A]	Lake Bungarby	Leaf compressions	Late Paleocene
E. microstoma [A]	Regatta Point	Leaf compression	Early Eocene
E. aberensis [AG]	Loch Aber	Mummified leaf fragments	Middle to Late Eocene
E. aberensis [G]	Little Rapid River	Mummified leaf fragments	Early Oligocene
E. sp. 'LRR1' [G]	Little Rapid River	Incomplete mummified capsule	Early Oligocene
E. mucronata [G]	Wilson's Creek	Leaf compression	?Latest Eocene-Early Oligocene
E. reticulata [G]	Lea River	Mummified capsule	Early Oligocene
E. leaensis [G]	Lea River	Mummified leaf fragment	Early Oligocene
E. sp. 'Leven' [G]	Leven River	Dispersed cuticle	Early Oligocene
E. lucida [G]	Regatta Point	Mummified leaves	Early Pleistocene
E. milliganii ssp. *milliganii* [G]	Regatta Point	Mummified leaves	Early Pleistocene
E. sp. [B]	Regatta Point	Dispersed cuticle	Early-Middle Pleistocene
E. lucida [DEG]	Regency Formation	Mummified leaves	Middle Pleistocene
E. milliganii ssp. *milliganii* [DEG]	Regency Formation	Mummified leaves	Middle Pleistocene
E. sp. [C]	Melaleuca Inlet	Dispersed cuticle	Late Pleistocene
E. lucida [F]	Pieman Dam	Mummified leaves	Late Pleistocene

[A] Hill (1991*a*); [B] Jordan *et al.* (1995); [C] Jordan *et al.* (1991); [D] Fitzsimons *et al.* (1990); [E] Jordan (1992); [F] Colhoun (1980); [G] this paper.

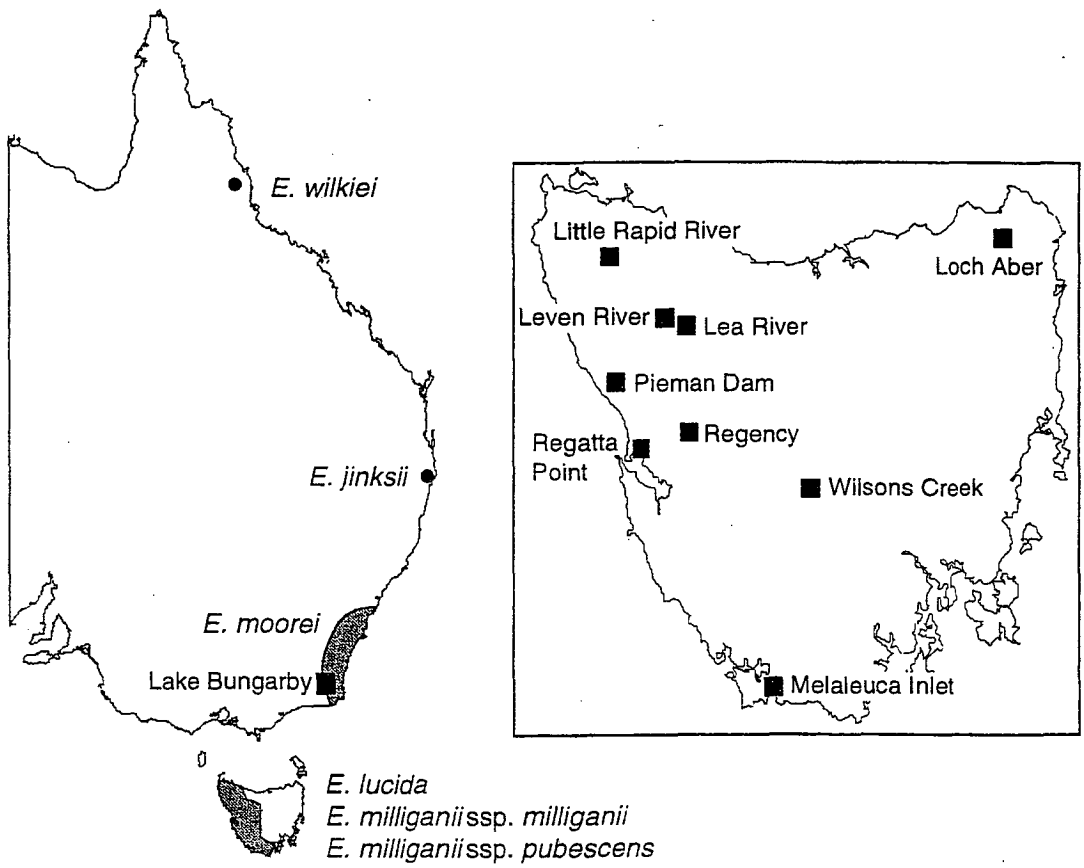
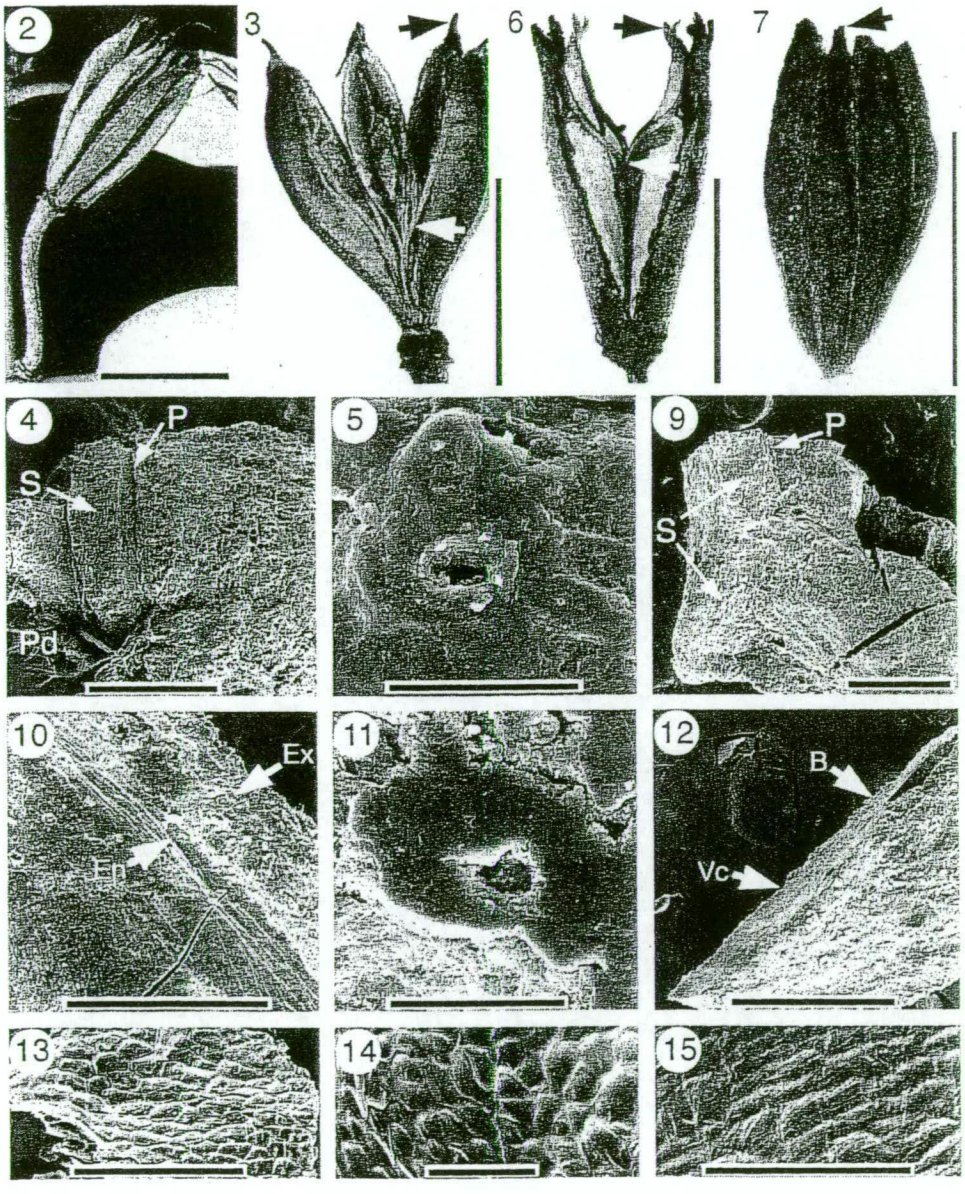

E. wilkiei
E. jinksii
E. moorei
Lake Bungarby
E. lucida
E. milliganii ssp. milliganii
E. milliganii ssp. pubescens
Little Rapid River
Loch Aber
Leven River
Lea River
Pieman Dam
Regency
Regatta Point
Wilsons Creek
Melaleuca Inlet

Fig. 1.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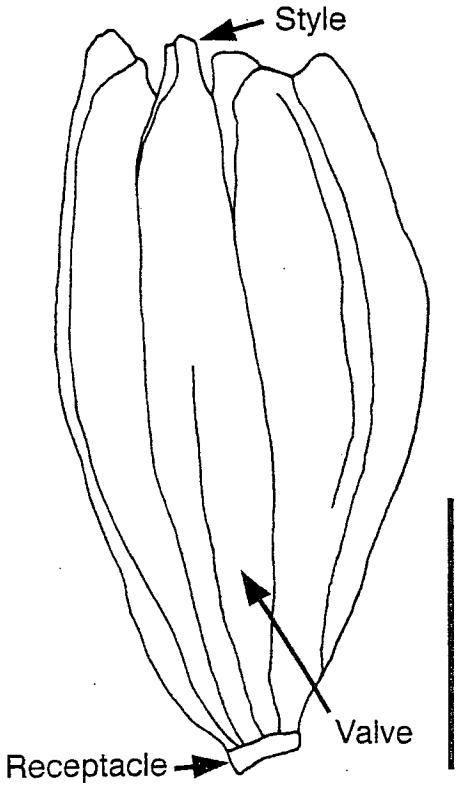
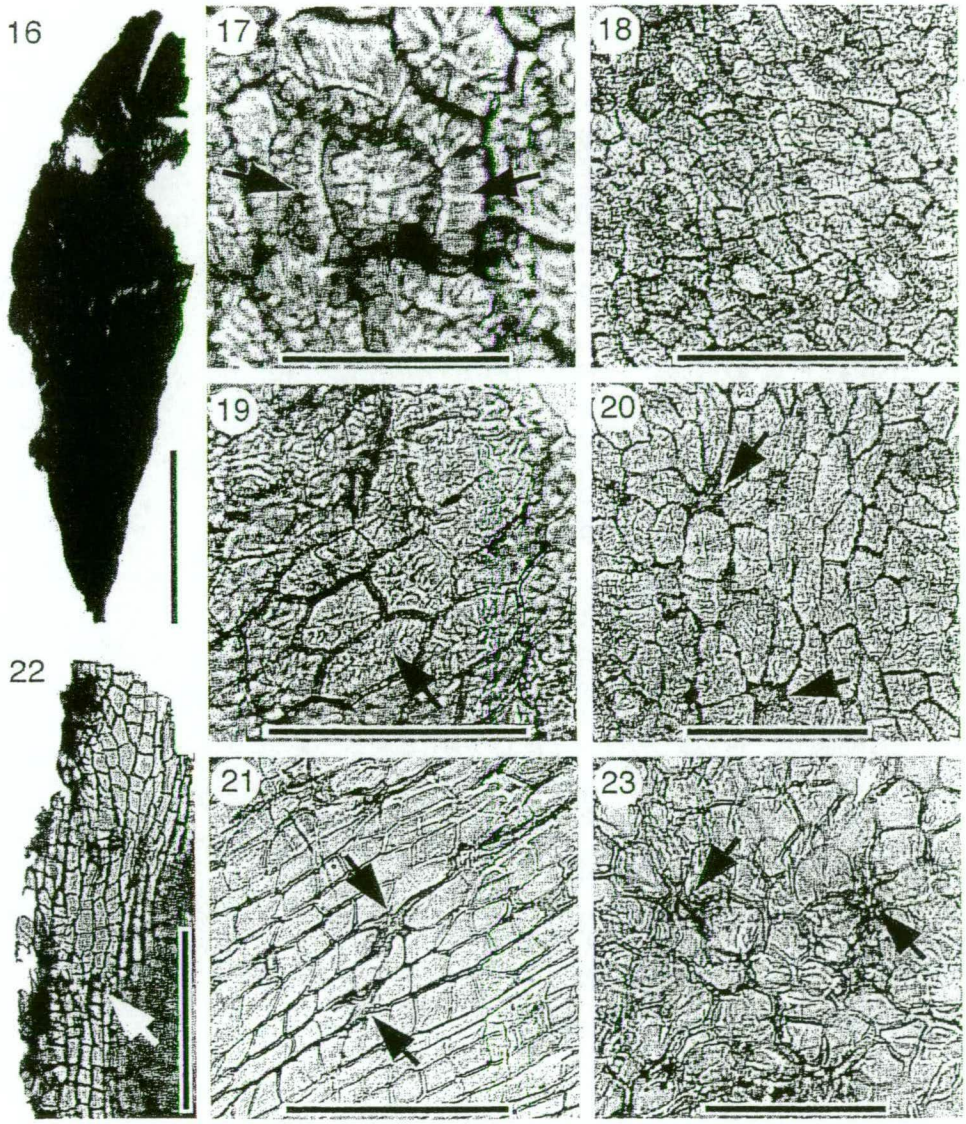


Fig. 8.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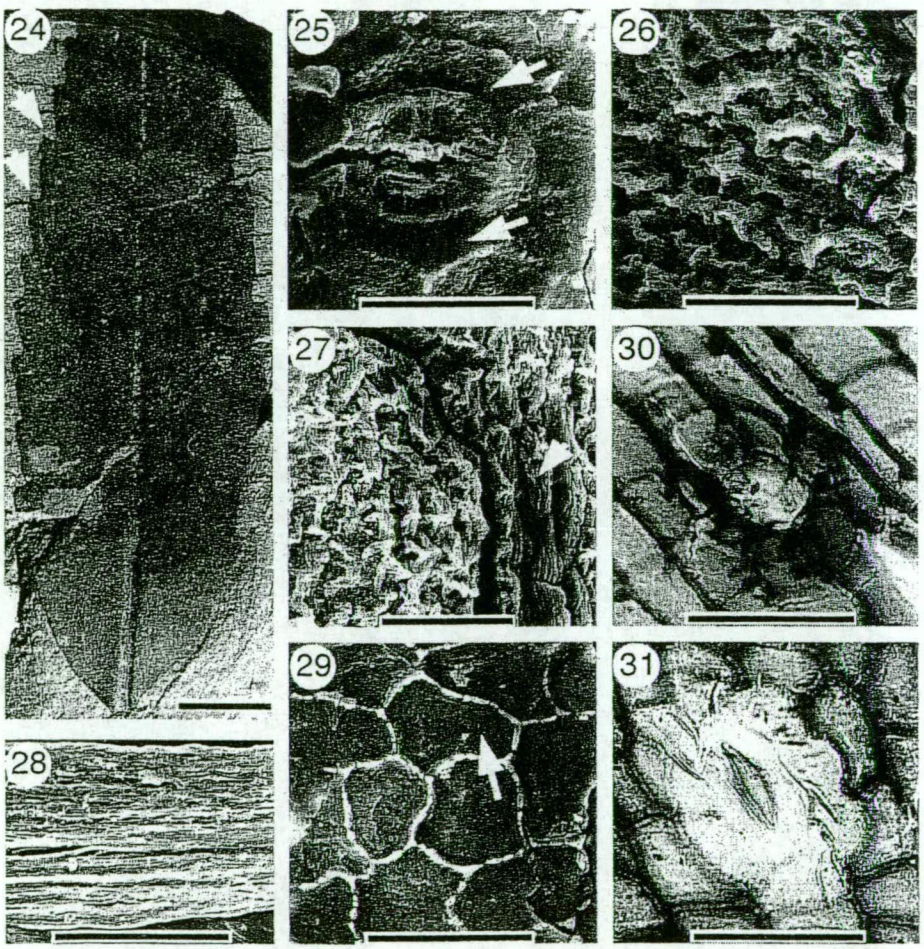
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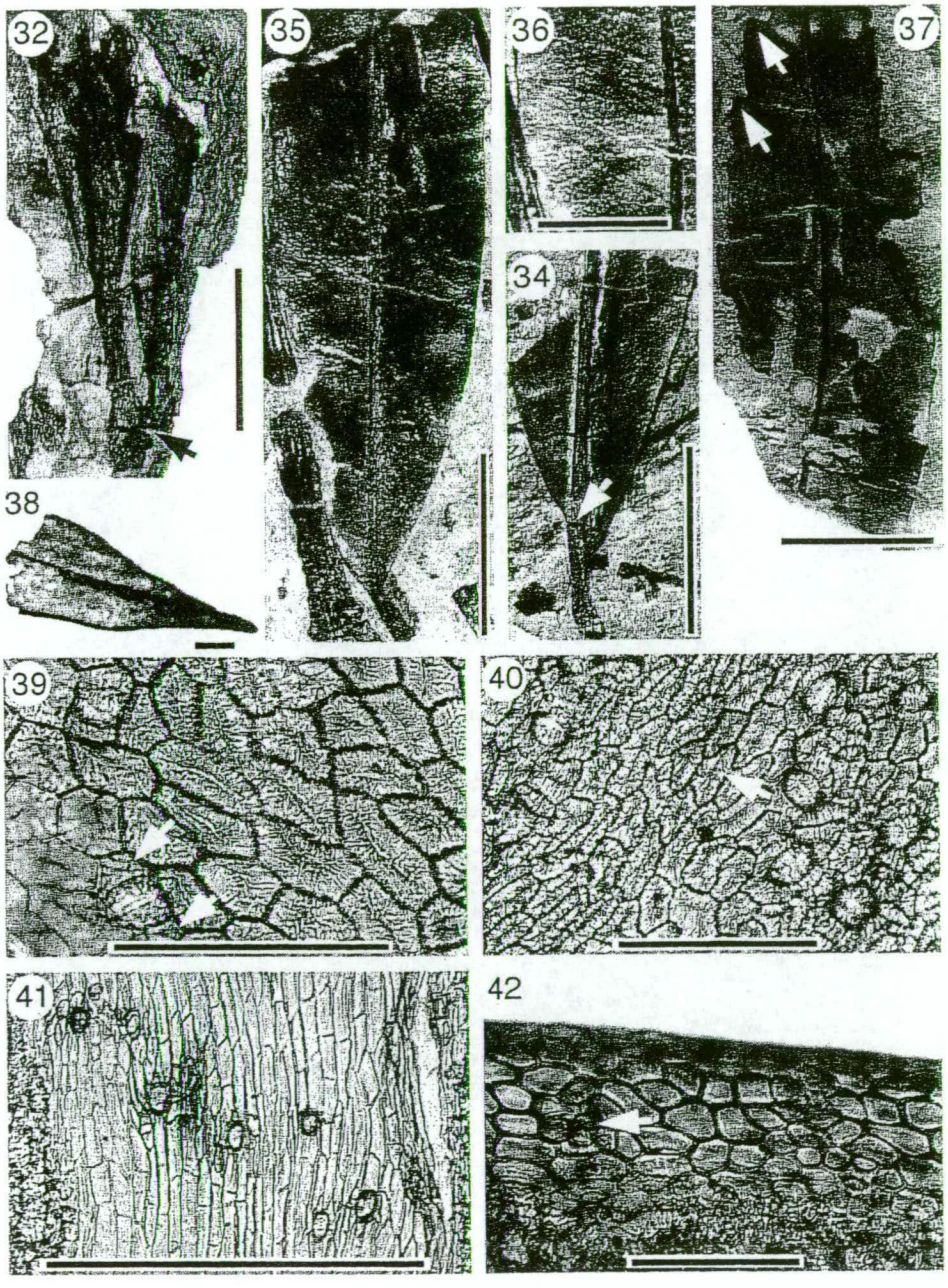
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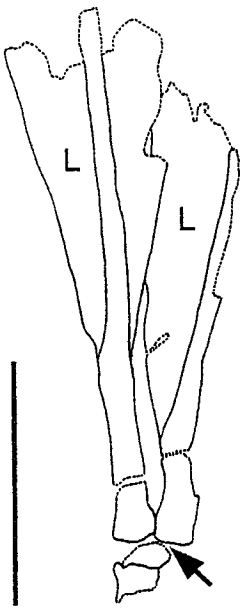
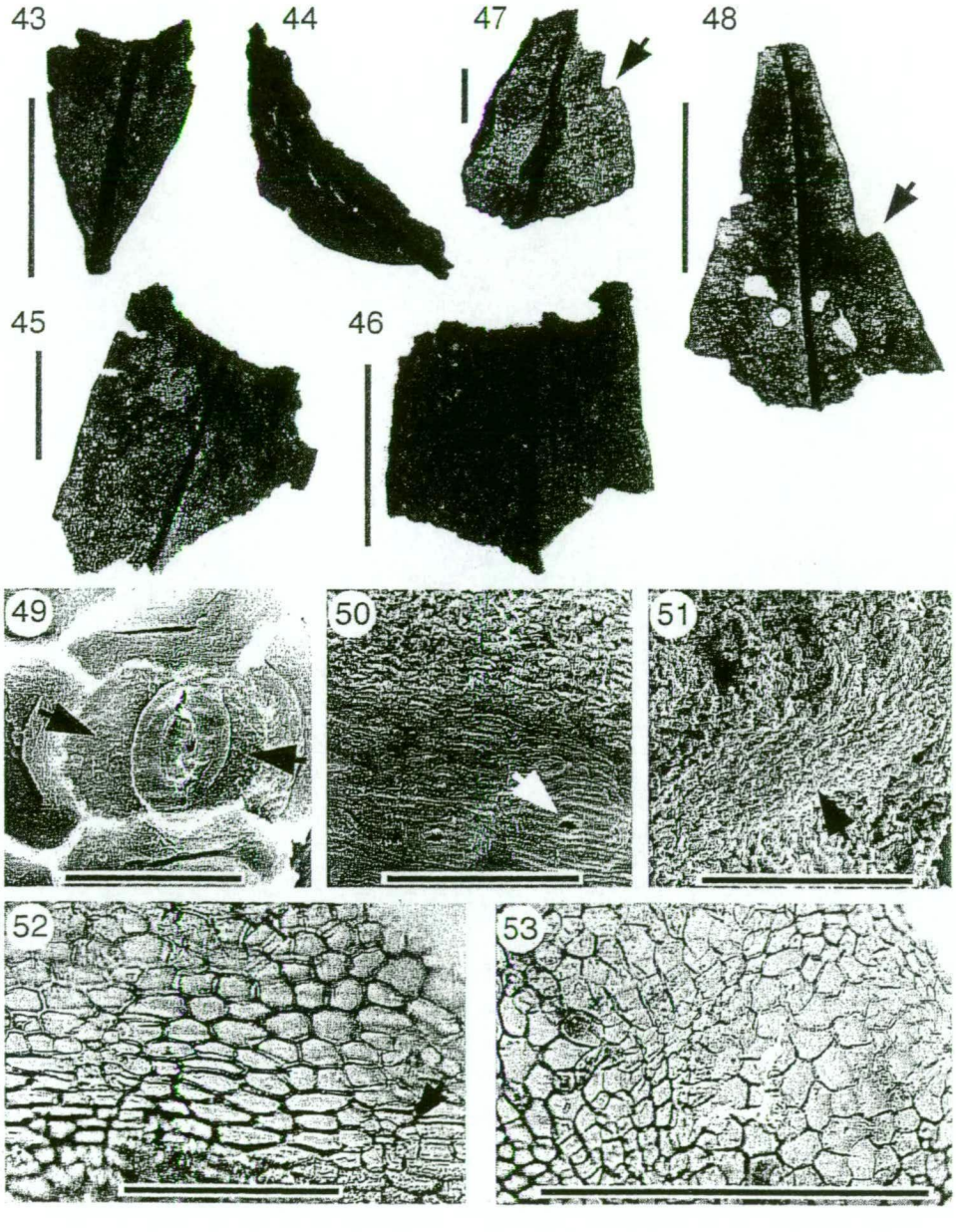


Fig. 33.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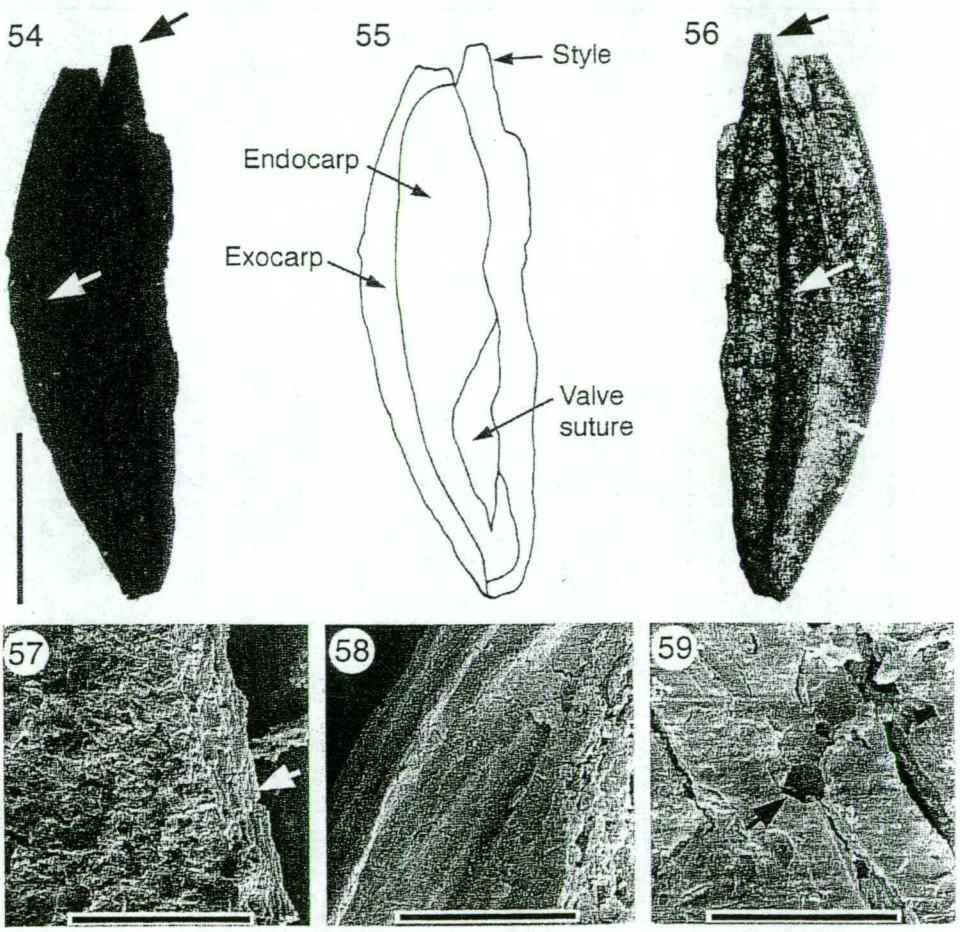
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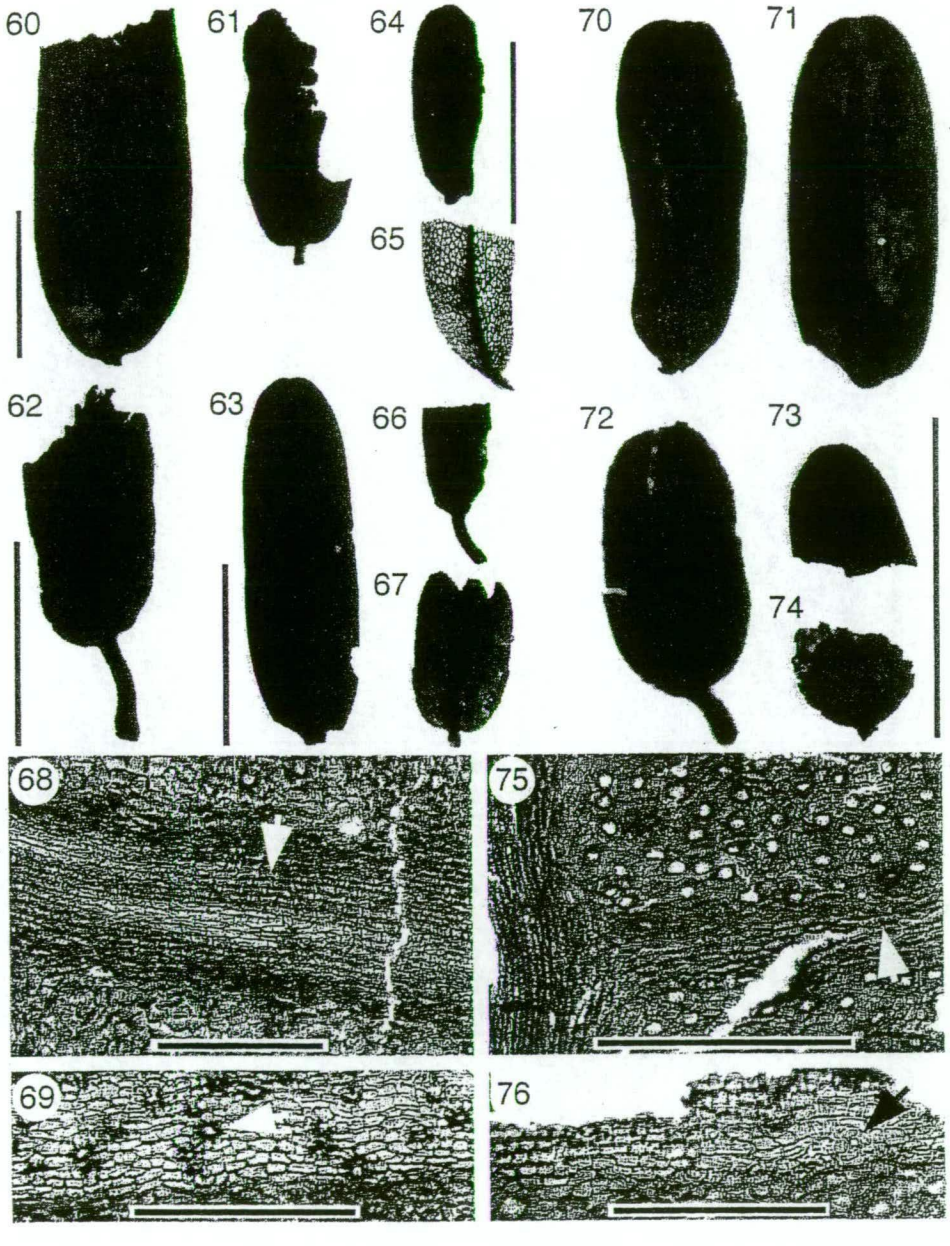
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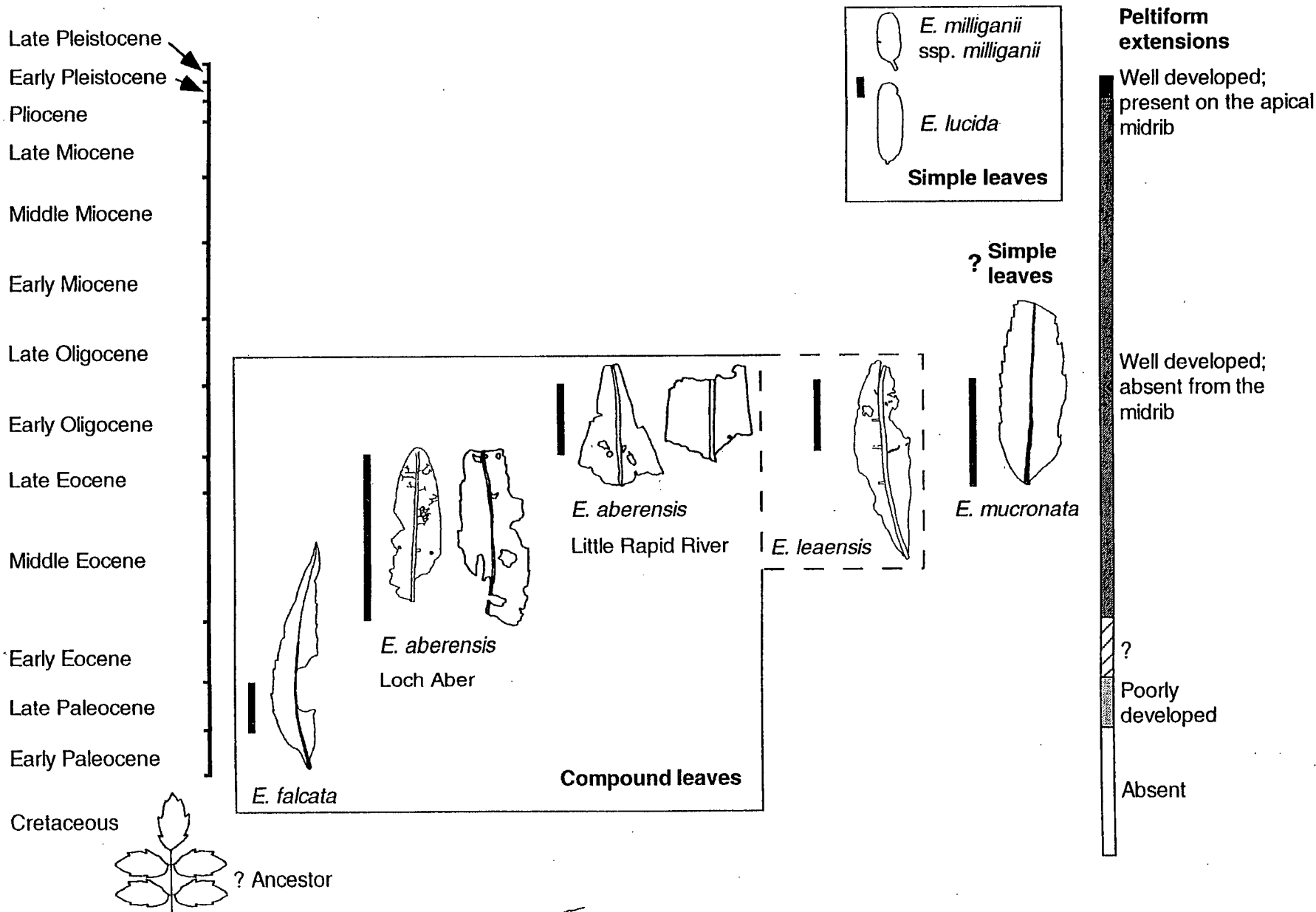
Late Pleistocene
Early Pleistocene
Pliocene
Late Miocene
Middle Miocene
Early Miocene
Late Oligocene
Early Oligocene
Late Eocene
Middle Eocene
Early Eocene
Late Paleocene
Early Paleocene
Cretaceous
? Ancestor
E. milliganii ssp. milliganii
E. lucida
Simple leaves
? Simple leaves
E. mucronata
E. leaensis
E. aberensis
Little Rapid River
E. aberensis
Loch Aber
E. falcata
Compound leaves
Peltiform extensions
Well developed; present on the apical midrib
Well developed; absent from the midrib
?
Poorly developed
Absent

Fig. 77

Comparative Morphology of *Anodopetalum* (Cunoniaceae)

Running title: Comparative Morphology of *Anodopetalum*

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Abstract

The vegetative and floral morphology of the Tasmanian endemic *Anodopetalum biglandulosum* is re-examined and illustrated. A detailed study of herbarium and fresh material identified a number of characters that have, in the past, been misinterpreted. The subsidiary cell arrangement around the stomates is brachyparacytic, and not anomocytic; the petals are shown to be notched, and not entire; the fruit is a weakly lignified, septicidally dehiscent capsule, not a berry, and the pollen is dicolporate, not tricolporate as has been previously reported. The two and three flowered inflorescences, and solitary flower are interpreted as a reduced cyme; while the leaf is interpreted as a unifoliolate compound leaf. The vegetative and floral morphology in *Anodopetalum* is compared with the closely related genera *Schizomeria*, *Platylophus* and *Ceratopetalum*. Features including notched/fringed petals, dicolporate pollen with a discontinuous (heterogeneous) tectum and weakly heterogeneous rays provide support for interpreting *Anodopetalum*, *Schizomeria*, *Platylophus* and *Ceratopetalum* as a monophyletic group. *Anodopetalum* differs from these genera in its strongly dehiscent fruits and winged seeds.

Introduction

The monotypic genus *Anodopetalum* is restricted to high rainfall areas of western and southern Tasmania (Fig. 1). The morphology of the single species, *A. biglandulosum* has been described by Hooker (1840), Bentham (1864), Mueller (1872), Rodway (1903), Curtis (1956) and Curtis and Stone (1967). Recent comparative studies in the Cunoniaceae, which included *Anodopetalum*, have focused on leaf morphology (Dickison 1975*a*), floral vascular anatomy (Dickison 1975*b*) and seed morphology (Dickison 1984). Wood anatomy of *Anodopetalum* has been well described by Dadswell and Eckersley (1938), Metcalfe and Chalk (1950), Ingle and Dadswell (1956) and Dickison (1980).

Although the genus has been examined in some detail by numerous authors, a considerable number of vegetative and reproductive characters have been described incorrectly, or inconsistently, in the literature. A phylogenetic study of the Cunoniaceae by Hufford and Dickison (1992), using several of these characters, placed *Anodopetalum* within a clade containing *Platylophus, Ceratopetalum, Codia* (including *Pullea*) and *Schizomeria*. The placement of *Codia* is considered incorrect, and it is probably more closely related to *Callicoma* and *Pullea sensu stricto*, based on recent molecular data (J. Bradford, pers. comm. 1999) and cuticular studies (Barnes and Hill in press).

This study re-examines the vegetative, floral and inflorescence morphology of *Anodopetalum*. Leaf and cuticle morphology are described and illustrated in detail for the first time, and scanning electron microscopy has provided additional information on floral features and fruit morphology. This study aims to collate the existing data on *Anodopetalum* and reappraise the phylogenetic significance of new and re-interpreted characters. In this study *Anodopetalum* is compared with the closely related genera *Platylophus, Ceratopetalum* and *Schizomeria*. These four genera will be referred to collectively as the *Schizomeria* clade.

Materials and Methods

Leaves, flowers and fruits were preserved in a 40% solution of FAA (5:5:90 formalin, acetic acid, alcohol). Leaves were cleared using the technique of Blackburn (1978). Leaf cuticles were prepared from a mid-lamina section placed in 10-50% hydrogen peroxide solution with several crystals of tetra-sodium pyrophosphate and warmed on a hot plate (30-35°C) for 24 h or until all other organic matter had oxidised. Prepared cuticles were rinsed in distilled water, stained in 1% aqueous safranin O and mounted in phenol glycerine jelly. Transverse leaf and petiole sections to a thickness of 10-25 μm were produced with a freeze microtome. Sections were stained with toluidine blue and mounted in phenol glycerine jelly. Cuticles and transverse sections were examined with a Zeiss Axioskop light microscope and photographed using a Canon EOS camera.

For scanning electron microscopy prepared cuticles, floral organs or pollen were either air dried or critical point dried, and placed onto aluminium stubs with carbon tape and sputter coated with gold to a thickness of 20 nm and examined with an Environmental Scanning Electron Microscope 2020 operated at 15-20 kV. Terminology follows Hickey (1979) for leaf architecture, Dilcher (1974) for cuticular morphology, Baranova (1987) for stomatal morphology and Erdtman (1952), Hideux and Ferguson (1976) and Moore *et al.* (1991) for pollen morphology. The studies were based largely upon Tasmanian (HO) collections, and samples collected in the field, and an appendix lists the material examined (Appendix 1).

Nomenclature

Anodopetalum A.Cunn. ex Endl. *Gen. Plant.* 2: 818 (1839): from the Greek *an* not *odous*; toothed, and *petalum*, petal; alluding to the supposed non-toothed nature of the petals. "A. Cunningham mss. 1829 in Herb Mus. caes." *fide* Endlicher *Gen. Plant.* 2: 818.

T: *Anodopetalum biglandulosum* (A. Cunn. ex Hook.) Hook. f.

Anodopetalum biglandulosum (A.Cunn. ex Hook.) Hook. f., *Flora Tasmaniae* 1: 148 (1856).

Weinmannia biglandulosa A.Cunn. ex Hook., *Icones Plantarum* 4: t.CCCI (1840); *Anodopetalum biglandulosum* (A.Cunn. ex Hook.) Hook. f. *Flora Tasmaniae* 1: 148 (1856); Curtis, The Student's Flora of Tasmania, Part 1: 176 (1956); Curtis and Stones, Endemic Flora of Tasmania, Part 1, p.46; Curtis and Morris Ed 2, Part 1: 180 (1975)

Anodopetalum glandulosum (A. Cunn. ex Endl.) Hook. f., *Histoire des Plantes* 3: 378 (1872) (Misspelling of *Anodopetalum biglandulosum*)

Typus: In damp shaded woods, Pine Cove, Macquarie Harbour, Van Diemen's Land (Tasmania), [~42^{0}11'S, 145^{0}22'E]; January 1819, A. Cunningham 97, a slender tree, 30 feet (~10 metres) high. (Lectotype: K [here designated] n.v., cibachrome at HO!, Fig. 2; Isolectotype: MEL!).

Illustrations: Hooker (1840) t CCI, Rodway (1903) p. 45, Curtis (1956) p. 176; Curtis and Stones (1967) p. 46.

Remarks

The hand written notes on the herbarium sheet (Fig. 2, left hand specimen) are likely to be Cunningham's original annotations and include his unpublished description of *Anodopetalum* . Endlicher (1839) in formally describing the genus *Anodopetalum* in *Gen. Plant.*, cited Cunningham mss. 1829 in Herb Mus. *caes* as the basis for the name. Hooker (1840) wrote that "I have hesitated whether or not there were characters sufficient to constitute a genus for this plant", and he chose instead to place it in *Weinmannia.*

Hooker (1840) went on to describe it as *Weinmannia biglandulosa*; the species name referring to the two bilobed glandular stipules. Cunningham's labels are clearly associated with the left hand specimen and it is designated (herein) as the Lectotype.

Hooker (1840) erroneously indicated that the plant was called "Native Beech", which is in error as Cunningham referred to it as "Native Birch" in the notes appended to the specimen. Neither name is now used, and the plant is commonly referred to as "Horizontal", due to its peculiar growth habit (see below).

Allan Cunningham collected the type of *Anodopetalum biglandulosum* from Pine Cove, on a trip to Macquarie Harbour with Captain King in 1819 (Heward 1842). Cunningham wrote "In no situation did I find the botany so novel and otherwise interesting as on the low shores of a little bight, about nine miles up from the entrance, called Pine Cove, from the abundance of Huon and Adventure Bay Pines, which its humid shaded woods afford. With the Huon Pine (which may be a *Dacrydium*, or altogether a new genus) and the named Adventure Bay Pine (*Podocarpus aspleniifolius* Lab.) [= *Phyllocladus aspleniifolius*], I detected the *Anopterus* of Labillardiere in flower, the *Cenarrhenes* of that author in fruit, the beautiful *Carpodontos* [= *Eucryphia*], the sassafras scented *Atherosperma moschatum*, the aromatic *Tasmannia* in fruit, the native birch, a species of *Weinmannia* (Footnote: *Weinmannia biglandulosa*, mss Hook. *Icon. Plant.* tCCC1), some of the Epacrideae, *Elaeocarpus pedunculatus* [= *Aristotelia pedunculata*], *Gaultheria hispida* in fruit with several others of like sterling importance".

Results

Distribution and Growth Habit

The species occurs in the high rainfall forests of western and southern Tasmania (Fig. 1), predominantly on nutrient poor soils derived from quartzite. It is relatively abundant in lowland habitats as a midstorey shrub to small tree, often falling into a horizontal position with prolific growth from side shoots. The peculiar growth habit of *Anodopetalum* has been studied by Barker and Brown (1994). Most specimens rarely attain a height of 8 m but in sheltered gullies with deeper soils trees can reach 12 m tall. Small populations of stunted or prostrate shrubs occur within the sub-alpine zone (< 1100 m a.s.l.) on mountain plateaux in south-western and western Tasmania.

Leaf Morphology and Venation

Leaves are opposite, unifoliolate, decussately arranged on the stem, or rarely occur in whorls of three in seedlings and coppice growth. The leaves are interpreted as unifoliolate, with a sessile leaflet attached to a petiole with a distinct articulation. Leaflets are leathery, most commonly elliptical to ovate lanceolate in shape, 5-18 mm wide, 15-60 mm long, with an obtuse to acute base and an acute apex (Fig. 3). Leaflets in shaded or coppice growth are occasionally bi- or tri-lobed (Figs 4-6), often to the extent where the lobes apparently form distinct leaflets (Fig. 5). The margin is regularly serrate (Figs 3-6) with glandular spherulate tooth apices, frequently with a spinose extension (Fig. 7). The petiole is ribbed along the adaxial margin forming furrows (Fig. 8), 2.0-10.0 mm long,

and slightly inflated at the stem and base of leaflet. Stipules are interpetiolar, caducous and bifid in shape, 2.0-6.0 mm long and 1.0-2.0 mm wide. Numerous glandular colleters are present on the adaxial surface of each stipule, and are often resinous in young growth.

The primary venation is pinnate (Fig. 3) or actinodromous in lobed leaflets (Figs 4-6). The midrib is straight to weakly sinuous in the apical region (Figs 3 and 9). Secondary veins alternate both sides of the midrib at a 45-50° angle, and loop to form a semicraspedodromous pattern, or terminate directly at a glandular sinus (Fig. 3). Multiple veins rarely originate from a single secondary loop and terminate at different sinuses. Tertiary venation is random reticulate with the presence of a weak composite intercostal vein (Fig. 3). Glandular, marginal tooth apices are vascularised by a vein originating from the sinus (Fig. 7). The ultimate venation near the leaf margin is incomplete with the weak development of a fimbrial vein (Fig. 7). Areolation is incomplete, with areoles pentagonal to quadrangular in shape (Fig. 10). Veinlets are once or twice branched and are enclosed in a sheath of sclerenchymatous cells with occasional terminal idioblasts (Fig. 11).

Cuticle Morphology

The abaxial external surface is smooth (Fig. 12) or in high altitude populations 'pitted' with the stomata slightly sunken (Fig. 13). Abaxial epidermal cells are isodiametric to pentagonal in shape and variable in size, mean length 18.4 μm and width 13.4 μm. Cell walls are slightly sinuous (Fig. 14) in low altitude populations, and less so in plants from higher altitudes or exposed habitats (Fig. 15). Epidermal cells on the major veins are elongate, linear with non-sinuous cell walls but are less conspicuous on minor veins and veinlets (e.g. Fig. 14).

Leaves are hypostomatic with stomata weakly arranged in areoles (Fig. 14). Stoma size is variable, 18.5-29.3 μm long (mean length 24.2 μm) and 16.9-21.5 μm wide (mean width 18.9 μm). Subsidiary cell arrangement is brachyparacytic (Figs 16-18) with the subsidiary cells positioned slightly above the guard cells (Figs 17 and 18). There is a t-piece at each stomatal pole (Fig. 16). Hydathodes have a brachyparacytic to stephanocytic arrangement and are present on the major veins and within some areoles in association with the stomata, mean length 31.6 μm and width 26.2 μm (Fig. 19).

The adaxial surface is smooth and non-ornamented (Fig. 20). Epidermal cells are isodiametric with straight walls. Venal cells are pentagonal to quadrangular and are slightly striate (Fig. 20). Unicellular, non-glandular trichomes are rare, but present on both surfaces, and are attached to a thickened foot cell which is surrounded by 5-7 radially modified epidermal cells (Figs 21 and 22).

Inflorescence, Floral and Fruit Morphology

The common condition in *Anodopetalum* is a solitary flower, or occasionally two to three flowers, in the uppermost leaf axils (Fig. 23). In those inflorescences consisting of three flowers the central flower is usually larger than the lateral ones, which would suggest that it is initiated first (Fig. 23). This pattern of flower maturation, with the lateral flowers being initiated after the central flower, and the arrangement of subtending bracts in a prophyllar position support interpretation of the three-flowered inflorescence in *Anodopetalum* as a dichasial unit (Figs 24 and 25). When there is a solitary flower there are a pair of subtending bracts (prophylls) midway along the axis which indicates that the solitary flower in *Anodopetalum* is derived from a very reduced cyme (Fig. 26).

The flowers are 4-merous, diplostemonous, and 4-8 mm long (Fig. 27). The 4 sepals are valvate, ovate in shape, 4-6 mm long, and have a fine indumentum over their inner surface. The 4 petals are thin, glabrous, lanceolate, 2-3 mm long, and divided distally, and are weakly notched (Fig. 27-29). This feature is most apparent in young buds, and is somewhat less obvious in the mature flower. The 8 stamens are attached by a moderately thin filament to a broad disk (torus) that surrounds the ovary (Fig. 27). The anthers are introrse, dorsifixed at just below the mid region of the anther, and weakly versatile (Figs 30 and 31). The anthers have a very long sterile distal connective protrusion, which is equivalent in length to the thecae (Figs 29-31). In bud, the anthers are oriented with the sterile thecal lobes vertical (Fig. 29), and in older flowers the distal connective protrusion is often flopped downwards (Fig. 31). The epidermal cells on the anthers are isomorphic, and variously shaped with little ornamentation (Fig. 29). The pollen grains are small (7-8.5 μm long; 4.7-5.5 μm wide), dicolporate and ellipsoid in shape (Figs 32 and 33). The tectum is partial, discontinuous and commonly absent in the interapertural zone (Fig. 33). Brochi are irregular and are absent from near the apertures, thereby forming a heterogeneous reticulate pattern. Muri are slightly thickened.

Anodopetalum has a bicarpellate glabrous ovary, with the carpels completely fused at the level of the ovary, and the thin styles are divergent and distally free (Fig. 27). Two ovules occur in each carpel, but often one, or both, may abort during development. The fruit in *Anodopetalum* is a capsule which is weakly lignified, coriaceous, ellipsoid in outline in dorsal view, convex in ventral view, 13-14 mm long and 5-6 mm wide (Figs 34 and 35). The lateral margins are strongly angled, while the dorsal surface is relatively flat with a slight ridge down the centre (Figs 34 and 35). The fruit is oval in transverse section. The capsule exhibits septicidal dehiscence, and splits open along the inner (ventral) surface. The sutural margin between the two carpels is clearly visible in the mature fruit, and the fruit splits completely apart (Fig. 34). The seeds are usually solitary, anatropous, obovate in outline, 5-6 mm long, non-winged (Figs 36 and 37), and have a finely reticulate surface (Fig. 38). The raphe extends longitudinally along the side of the seed (Figs 36 and 37). The seeds are shed within a papery layer of tissue, which is

formed from the inner wall of each carpel. This thin papery layer, which is 13-14 mm long and 5-6 mm wide, is distinct from the seed and forms a wing-like envelope around the seed.

Discussion

This re-examination of the vegetative and reproductive morphology of *Anodopetalum,* and closely related taxa in the *Schizomeria* clade, has identified a number of characters that have been previously misinterpreted. Compound leaves are common in Cunoniaceae, with leaflet reduction probably occurring within several different lineages (Hufford and Dickison 1992). The leaf in *Anodopetalum* has been invariably interpreted as a single or unifoliate leaf (Hooker 1840; Bentham 1864; Curtis 1956; Hufford and Dickison 1992). We interpret the articulation at the base of the leaf, and the occasionally lobed condition in coppice growth or shade leaves, as evidence that *Anodopetalum* has a reduced compound leaf consisting of a single terminal leaflet, and is therefore unifoliolate. It seems likely that the leaf of *Anodopetalum* has been reduced from a trifoliolate leaf, probably similar to those present in *Platylophus* and most species of *Ceratopetalum*. *Schizomeria* differs from these genera in having simple leaves.

Sclerenchymatous veinlet sheathing was considered to occur only in some *Schizomeria* species by Hufford and Dickison (1992), however this study shows it is also the condition in *Ceratopetalum* and *Anodopetalum* (Table 1). Dickison (1975*a*) and Hufford and Dickison (1992) interpreted the stomatal morphology of *Anodopetalum*, and related genera, to be anomocytic. Detailed examination of the stomatal apparatus with scanning electron microscopy (Fig. 16) and transverse leaf sections (Figs 17 and 18) clearly illustrate a brachyparacytic arrangement of subsidiary cells in *Anodopetalum*. This is also the common condition within the *Schizomeria* clade (Table 1) and some other Cunoniaceae genera (e.g. *Eucryphia, Aistopetalum*, *Acsmithia* and *Ackama*). New observations for *Anodopetalum* include the incomplete formation of a fimbrial vein and a t-piece at each stomatal pole. *Schizomeria, Ceratopetalum* and *Platylophus* all possess a well developed fimbrial vein and have a t-piece at each stomatal pole.

Hufford and Dickison (1992) considered that *Anodopetalum* has solitary flowers, although occasionally three flowered inflorescences occur, and were recorded by Curtis and Morris (1975). The presence of prophylls in both solitary and three-flowered inflorescences, and the pattern of flower maturation, are consistent with interpreting the inflorescences as a strongly reduced dichasial inflorescence. *Anodopetalum* inflorescences are axillary, which is the common condition in the *Schizomeria* clade, except for some *Ceratopetalum* and *Schizomeria* species where the inflorescences may also be terminal (Hoogland 1960; Hufford and Dickison 1992; H. C. Fortune Hopkins pers. comm. 1999).

Examination of herbarium collections in HO demonstrates that the flowers are consistently four-merous, and records of the flowers being five-merous (Bentham 1864; Baillon 1872; Rodway 1903; Curtis 1956) appear to be in error. The flowers of *Anodopetalum* and other genera in the *Schizomeria* clade exhibit valvate aestivation, which was considered to be the plesiomorphic condition in the Cunoniaceae (Hufford and Dickison 1992). The petals in *Anodopetalum* have been invariably described as "entire" in all previous studies. The generic name *Anodopetalum*, from the latin *an*: not, *odous*: toothed, and *petalum*: petal; alludes to the supposed non-toothed nature of the petals. Studies of buds, using scanning electron microscopy, demonstrate that the petals are distally notched (Fig. 29). This is a significant character as the petals of *Schizomeria*, *Platylophus*, and the only species in *Ceratopetalum* with petals, *C. gummiferum* Sm., also have distally fringed (notched) petals which further supports a close relationship between these four genera. The petals in all other petalous Cunoniaceae genera are entire with the exception of *Gillbeea*, which has unusally notched petals with apical glands (Engler 1928; Hoogland 1960; Dickison 1989). The autapomorph of apical glands in *Gillbeea* and the phylogeny of Hufford and Dickison (1992) both support a polyphyletic origin of notched/fringed petals in *Gillbeea* and the *Schizomeria* clade. Hufford and Dickison (1992) noted that the phylogenetic significance of the variation in petal shape within the family required additional study.

The stamens in *Anodopetalum* are typically introrse, dorsifixed, with the relatively thin filament attached at, or near, the midpoint of the anther. Nearly all Cunoniaceae and *Davidsonia*, except *Aphanopetalum*, have this arrangement (Endress and Stumpf 1991). *Anodopetalum* stamens have a very long sterile connective protrusion, which is also a feature that occurs to a lesser extent in other genera of the *Schizomeria* clade, and in several other Cunoniaceae genera, such as *Ackama, Vesselowskya* and *Opocunonia*. The pollen of *Anodopetalum* is dicolporate and not tricolporate as interpreted by Hufford and Dickison (1992). A heterogeneous tectum that is at least partially discontinuous in the interapertural zone is the common condition within the *Schizomeria* clade. Hideux and Ferguson (1976), in a phenetic analysis using pollen morphology characters, also supported a close similarity between these four genera.

Most genera in the Cunoniaceae have flowers that are hypogynous or slightly epigynous, and this is true for genera in the *Schizomeria* clade, except for *Ceratopetalum* which is strongly epigynous (Hufford and Dickison 1992). The disk (torus) is annular in *Anodopetalum*, *Ceratopetalum*, and *Platylophus* but segmented in *Schizomeria*. The fruits in *Anodopetalum* are bilocular with two ovules per carpel (Hooker 1840). Bicarpellate fruits are the common condition within the clade and most genera have two or fewer ovules in each carpel. Some *Schizomeria* species can have three or four ovules per carpel (H. C. Fortune Hopkins pers. comm. 1999). The fruits of *Anodopetalum* have been variously described as fleshy (Bentham 1864; Rodway 1903; Curtis 1956), berries

(Dickison 1984; Hufford and Dickison 1992), capsules (Hooker 1856) and septicidal capsules (Mueller 1872). Dickison (1984) in the most recent study interpreted the fruits as berries and indehiscent, but his observations were from a single herbarium collection (Webb 3337) in Brisbane (BRI AQ310367) that only possessed immature fruits. Herbarium collections in Hobart (HO 406179, HO 406293) show the fruit is a perfectly dehiscent, septicidal, weakly lignified capsule, with the valves splitting open completely to release one or rarely two seeds. Mueller (1872, p. 272) reached the same conclusion when he described the fruits as "*Tali modo habes quasi capsulam perfecte septicide biloculatam et iterum luculicide profunde fissam*". Dickison (1975*b*) showed that the ovular traces were separate below the level of placentation, and that there was a ventral suture above the level of placentation in *Anodopetalum* carpels. Each seed is released in a wing-like envelope of tissue derived from the inner wall of each carpel. The entire inner wall of the carpel has been modified for dispersal. The fruits of *Anodopetalum* differ from the other genera in the *Schizomeria* clade in being dehiscent. The other three genera have either indehiscent or tardily dehiscent fruits (*Ceratopetalum* and *Platylophus*) or drupes (*Schizomeria*). The seed surface in *Anodopetalum* has a fine reticulate appearance. The seed surface appears weakly striate in *Ceratopetalum succirubrum* C. T. White and *Schizomeria ovata* D. Don, and finely reticulate in *Platylophus* (A. C. Rozefelds, unpubl. data).

Morphological characters that are misinterpreted or poorly understood may interfere with the definition of coherent and phylogenetically meaningful higher taxa. This is particularly the case with the Cunoniaceae where the family limits are still somewhat controversial and the placement of some genera, e.g., *Davidsonia*, *Bauera* and *Aphanopetalum*, within the higher rosids is unclear (Hufford and Dickison 1992; Dickison *et al.* 1994). While this study identifies some characters that have been misinterpreted, it also reiterates much of the earlier work undertaken. *Anodopetalum* has opposite decussate compound leaves with glandular tooth apices, adaxial stipular colleters, a brachyparacytic subsidiary cell arrangement, valvate calyx aestivation, a distal anther connective protrusion, and vessels often in radial multiples which are features shared with many genera in the Cunoniaceae. *Anodopetalum* shares with *Schizomeria*, *Platylophus* and *Ceratopetalum* a number of vegetative and floral characters (Table 1), including the notched/fringed petals, dicolporate pollen with a discontinuous (heterogeneous) tectum (Hideux and Ferguson 1976), and weakly heterogeneous wood rays (Ingle and Dadswell 1956) that collectively support a close phylogenetic relationship between these genera. *Anodopetalum* differs from these genera in the perfectly dehiscent fruits, and the method of seed dispersal which appears to be unique within the family.

Acknowledgments

We thank Ken Hill, the Australian Botanical Liaison Officer (1997-1998), for arranging a cibachrome of the lectotype of *Anodopetalum* to be made available (Fig. 2 herein). Helen Fortune Hopkins provided photocopies of Hoogland's notes at P which have been invaluable in bringing to our attention important literature that is not easily available in Tasmania. Helen Fortune Hopkins, and two anonymous reviewers, also provided useful comments on the manuscript. Funding to undertake this study was provided by the Australian Biological Resources Survey towards the Flora of Australia Project (ACR) and an Australian Postgraduate Award (RWB). Access to Critical Point Driers was provided by the Australian Antarctic Division (Anna Macadie) and Department of Agricultural Science (Phillip Brown). Scanning electron microscopy facilities were provided through the Central Science Laboratories, University of Tasmania (David Steele). We thank the staff at AD, CANB, K, MEL, NSW and PERTH for the loan of additional specimens, or for providing photographs of material in their collections. Ms Belinda Pellow provided technical support for this project.

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Fig. 1. Map of Tasmania (left) showing the distribution of *Anodopetalum biglandulosum* based upon Tasmanian Herbarium (HO) records. The species occurs from sea level to the subalpine (<1100 m a.s.l.) zone across its entire range. The geographic position of Tasmania relative to mainland Autsralia is also shown (right).

Fig. 2. Photograph of the Lectotype of *Anodopetalum biglandulosum* (Cunningham 97, K). Lectotype is the specimen on the far left with Cunningham's generic description of *Anodopetalum.*

Figs 3-11. Leaflet form, venation and petiole anatomy in *Anodopetalum biglandulosum.* **Fig. 3.** Cleared unifoliolate showing venation. Scale bar = 10 mm. **Figs 4-6.** Variations in leaflet form. **Fig. 4.** Tri-lobed leaflet. **Fig. 5.** Tri-lobed leaflet showing almost complete lobe differentiation into a separate leaflet (arrow). **Fig. 6.** Bi-lobed leaf formed by asymmetrical development. Scale bar for all = 10 mm. **Fig. 7.** Light micrograph showing tooth vascularisation. Note the presence of a spinose extension (S) on the glandular tooth apices and poor fimbrial vein (F) development. Scale bar = 3 mm. **Fig. 8.** Transverse section of the petiole showing adaxial furrows (arrows). Scale bar = 300 μm. **Fig. 9.** Apical region of a cleared leaflet showing weakly sinuous midrib (arrow). Scale bar = 10 mm. **Fig. 10.** Incomplete areolation with branching veinlets. Scale bar = 1 mm. **Fig. 11.** Veinlets with sclerenchymatous sheath and terminal idioblasts (arrows). Scale bar = 250 μm.

Figs 12-22. Light and scanning electron micrographs of the cuticle and stomatal apparatus of *Anodopetalum biglandulosum*. **Figs 12-15.** Abaxial cuticle. **Fig. 12.** Smooth outer surface with superficial stomata. Scale bar = 150 μm. **Fig. 13.** 'Pitted' outer surface with stomata slightly sunken. Scale bar = 150 μm. **Fig. 14.** Large epidermal cells with sinuous walls. Note stomata in weak areoles. Scale bar = 200 μm. **Fig. 15.** Small epidermal cells with straight walls. Scale bar = 200 μm. **Fig. 16.** Inner abaxial cuticle showing position of guard cells (G), brachyparacytic subsidiary cell arrangement (S) and a t-piece (T) at each pole. Scale bar = 20 μm. **Fig. 17.** Transverse leaf section showing stomatal apparatus. Note that the subsidiary cells (S) occur slightly above the guard cells (G), and adjacent epidermal cells (E). Scale bar = 20 μm. **Fig. 19.** Abaxial cuticle showing a hydathode (left) and stoma (right). Scale bar = 25 μm. **Fig. 20.** Adaxial cuticle showing weakly striated venal cells. Scale bar = 200 μm. **Fig. 21.** Inner abaxial cuticle showing a single hair base with radially modified basal cells and a central foot cell. Scale bar = 35 μm. **Fig. 22.** Single trichome base showing basal thickening around the foot cell (arrow). Scale bar = 40 μm.

Fig. 18. Line drawing of the stomatal apparatus illustrated in Fig. 17 showing the overlying position of the subsidiary cells (S), guard cells (G) and adjacent epidermal cells (E). A thick cuticle (C) is present with a wax layer (W).

Figs 23-33. Inflorescence, floral and pollen morphology of *Anodopetalum biglandulosum.* **Fig. 23.** Three flowered dichasium. Scale bar = 5 mm. **Fig. 24.** Line drawing of the three flowered dichasium in figure 23 showing the position of prophylls (arrows). **Figs 25, 26.** Models of the inflorescence structure showing the arrangement of flowers and prophylls. **Fig. 25.** Three flowered inflorescence. **Fig. 26.** Single flower inflorescence. **Figs 27-31.** Scanning electron micrographs of flowers, buds and anthers. **Fig. 27.** Mature flower showing arrangement of sepals and small petals. Scale bar = 1 mm. **Fig. 28.** Partially dissected unopened flower bud showing the arrangement of stamens (A) and distally notched petals (P). Scale bar = 1 mm. **Fig. 29.** Detail of stamens (A) and petals (P) showing distinct notches in the apical region (arrows). Scale bar = 500 μm. **Figs 30, 31.** Anther morphology. **Fig. 30.** Dorsal view showing longitudinal anther dehiscence and long sterile connective protrusion. Scale bar = 500 μm. **Fig. 31.** Ventral view showing the filament attachment to the anther. Scale bar = 400 μm. **Figs 32, 33.** Scanning electron micrographs of pollen grains. **Fig. 32.** Dicolporate ellipsoid grains. **Fig. 33.** Pollen grains showing the discontinuous, heterogeneous tectum that is absent in the inter-aperatural zone. Scale bar for Figs 32, 33 = 5 μm.

Figs 34-36. Line drawings of the fruit and seed morphology of *Anodopetalum biglandulosum.* **Figs 34, 35.** Mature fruit morphology. **Fig. 34.** Ventral view showing the sutural margin (arrows) between the two carpels. **Fig. 35.** Dorsal view. Scale bar for both = 10 mm. **Fig. 36.** Anatropous seed showing the position of the raphe (arrow). Note the aborted second ovule (right). Scale bar = 1 mm. **Figs 37, 38.** Scanning electron micrographs of the seed of *A. biglandulosum.* **Fig. 37.** Mature seed. Scale bar = 1 mm. **Fig. 38.** Detail of the seed coat showing the fine reticulate pattern. Scale bar = 150 μm.

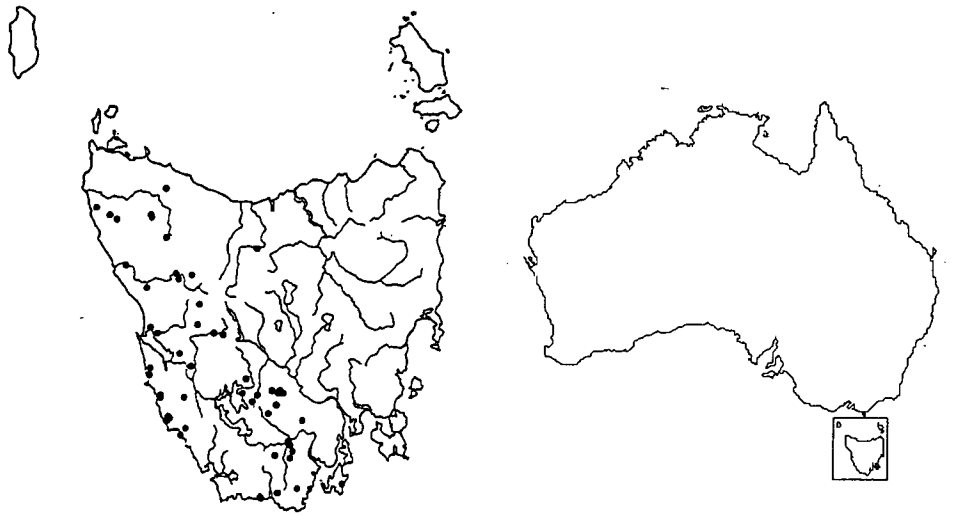


Fig. 1.

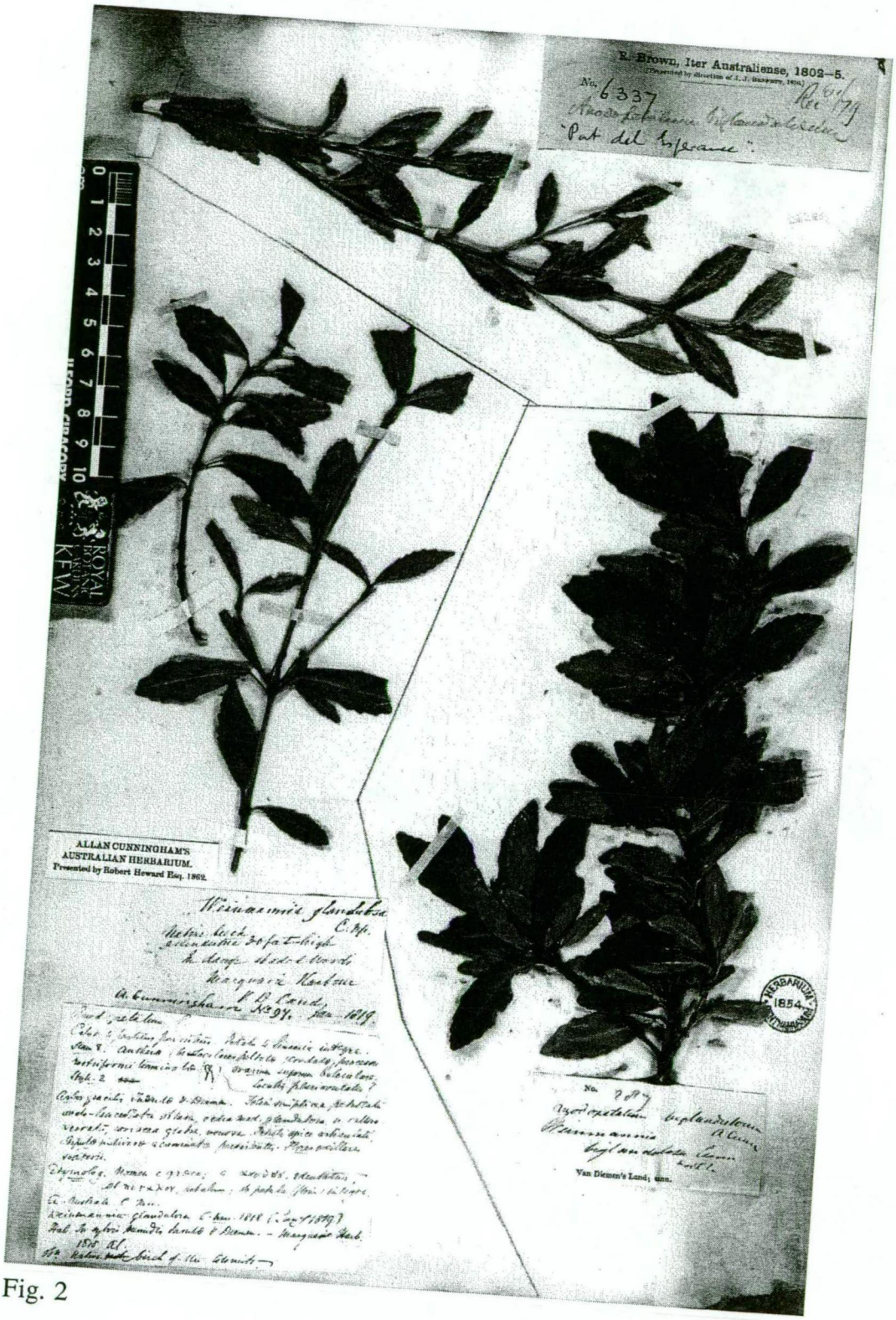
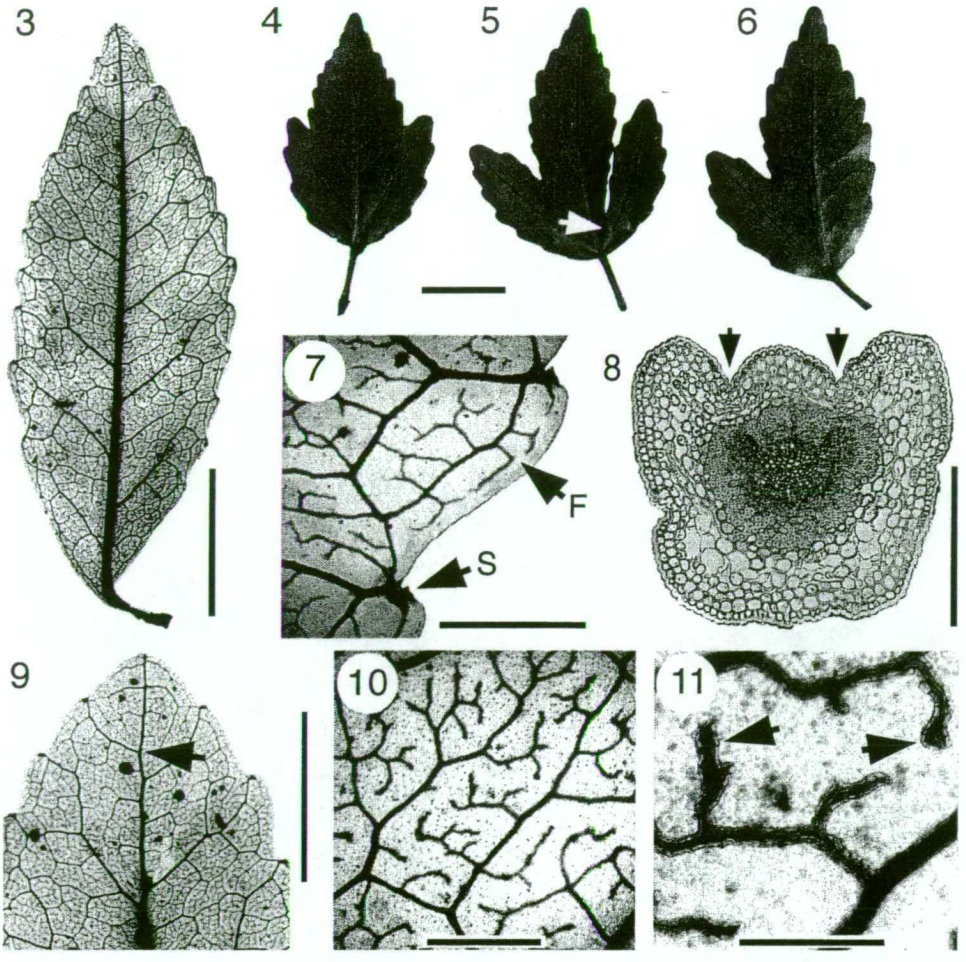
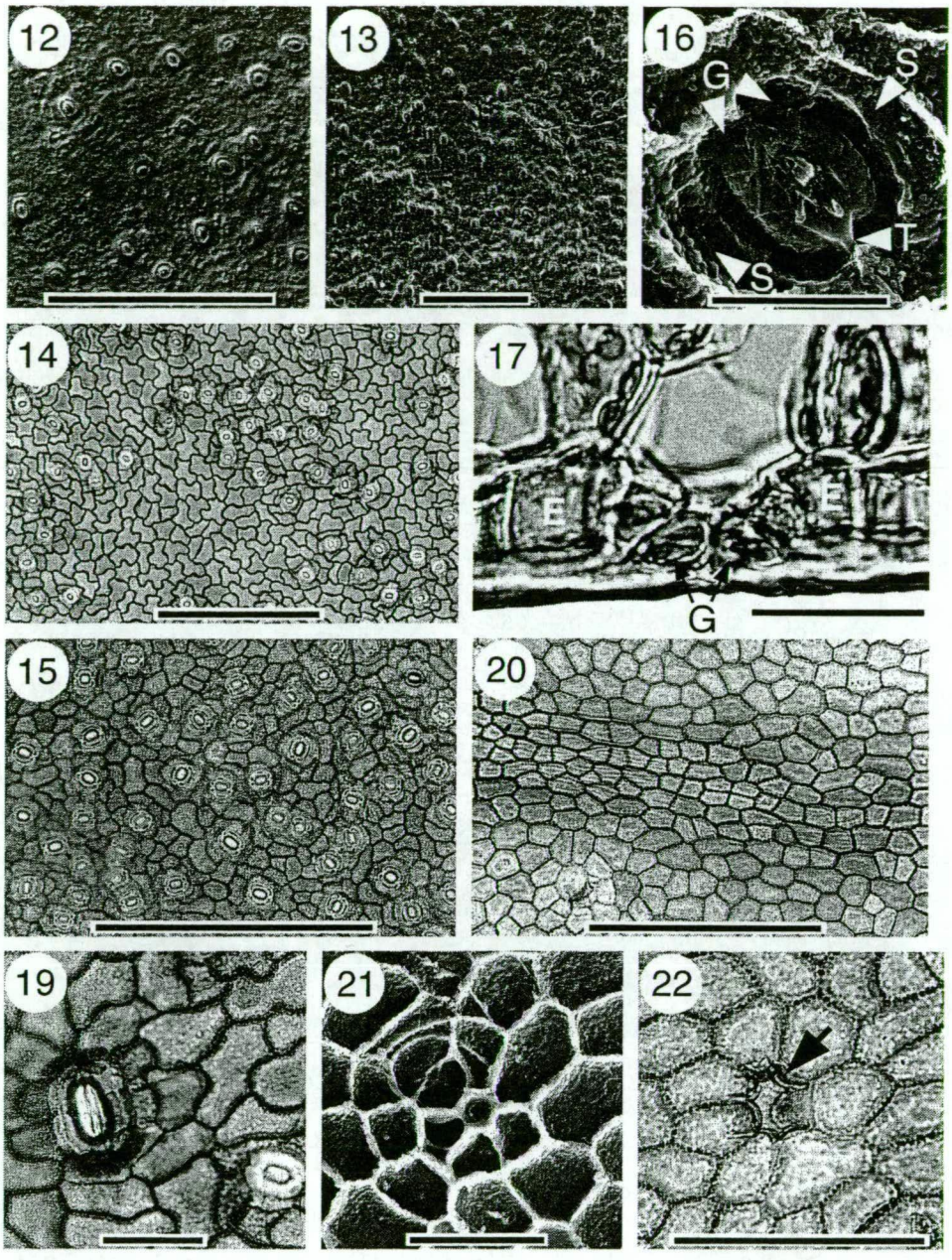

R. Brown, Iter Australiense, 1802–5.
No. 6337
ALLAN CUNNINGHAM'S
AUSTRALIAN HERBARIUM.
Presented by Robert Heward Esq. 1862.
Van Diemen's Land; unn.
HERBARIUM
1854

Fig. 2



Figs 3-11.



Figs 12-22

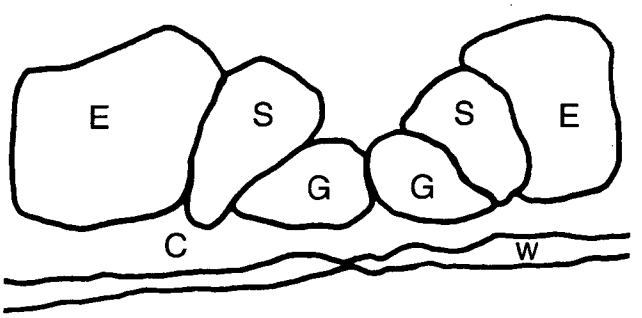
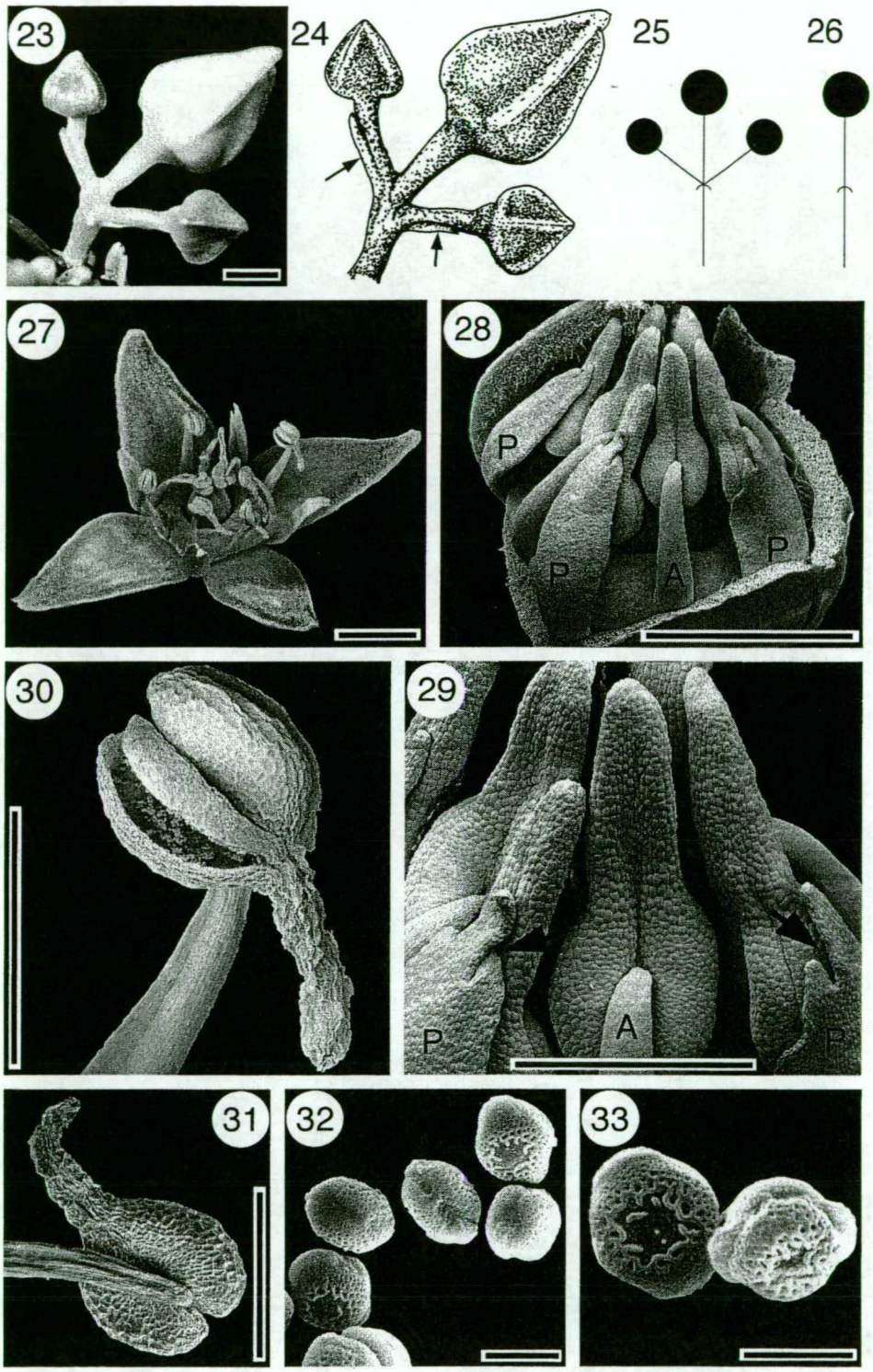


Fig. 18



Figs 23-33

Appendix 1. Specimens of *Anodopetalum biglandulosum* examined during this study

Locality altitudes are indicated where available.

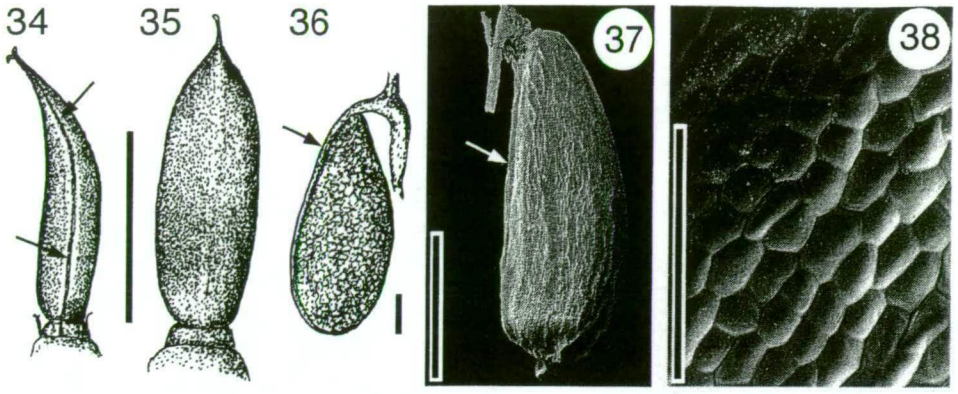
Collection	Locality	Collector and number	Characters examined
HO 28671	Lake Vera, Frenchmans Cap National Park	S.J.Berrigan s.n.	Leaf, flower, fruit measurements
HO 88954	Track up NE ridge of Mt. Anne, 700 m a.s.l.	A.M.Buchanan 5149	Leaf, flower, fruit measurements
HO 89938	Landing Creek, Birchs Inlet, 20 m a.s.l.	A.M.Buchanan 1962	Leaf, flower, fruit measurements
HO 92344	Above Lady Barron Falls, Mt. Field National Park 210 m a.s.l.	H.F.Comber s.n.	Leaf, flower, fruit measurements
HO 117363	South Ridge of Mt. Dundas, 600 m a.s.l.	P.Collier 2131	Leaf, flower, fruit measurements
HO 144812	Near Leaning Tea Tree saddle, 840 m a.s.l.	A.M.Buchanan 11341	Leaf, flower, fruit measurements
HO 403505	Rapid River, 390 m a.s.l.	A.Moscal 7308	Leaf, flower, fruit measurements
HO 404707	Farm Creek at Pieman Road, 170 m a.s.l.	A.M.Buchanan 9809	Leaf, flower, fruit measurements
HO 405943	North Branch of Midway Creek, South Bruny Island, 170 m a.s.l.	A.M.Buchanan 8387	Leaf, flower, fruit measurements
HO 406179	Wanderer River, 6 kms up from North	A.M.Buchanan 6224	Fruits
HO 406293	3 km S. of Mt. Osmund, 100 m a.s.l.	A.M.Buchanan 6017	Fruits
HO 408812	Frankland River, 1 km N. of Balfour, 120 m a.s.l.	A.Moscal 4766	Leaf, flower, fruit measurements
HO 412235	Headwaters of Jones Creek, on track N. of Hibbs Lagoon, 100 m a.s.l.	A.M.Buchanan 1867	Leaf, flower, fruit measurements
Barnes Coll.	King River, 40 m a.s.l.	R.Barnes s.n., (spirit)	Flowers
Barnes Coll.	Teepookana Forest Reserve, south of Strahan, 220 m a.s.l.	R.Barnes s.n., (spirit)	Leaf and fruit measurements

Barnes Coll.	Arve Picnic area, Arve Valley, 160 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Lake Johnston, Mt. Read, 900 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Base of Adamsons Peak Track, 170 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Clear Hill Road, Lake Gordon, 770 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Creepy Crawly Nature Trail, 540 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Holley Road, Lake Gordon, 360 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Serpentine Dam, Lake Pedder, 410 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Franklin River, as it crosses the Lyell Highway, 410 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Henty Dam, western Tasmania, 520 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Base of Lake Skinner Track, 520 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Lake Dove, Cradle Mt. National Park, 930 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Near summit of Mt. Wedge, 870 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Sentinel Range, Lake Pedder, 900 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Luina, north-western Tasmania, 320 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Bird River, 80 m a.s.l.	R.Barnes s.n.	Leaves
Barnes Coll.	Base of Frenchmans Cap walking track, 390 m a.s.l.	R.Barnes s.n.	Leaves
Rozefelds Coll.	Mt. Field National Park, 210 m a.s.l.	A.C.Rozefelds 466, (spirit)	Flowers

Table 1. Comparative morphology of *Anodopetalum* and the closely related genera *Ceratopetalum, Schizomeria* and *Platylophus*. Sources: Vegetative characters: R. Barnes pers. obs.; Reproductive characters: A.C. Rozefelds and R. Barnes pers. obs. and Hufford and Dickison (1992); Wood characters: Dadswell and Eckersley (1938), Ingle and Dadswell (1956) and Dickison (1980).

	Anodopetalum	*Ceratopetalum*	*Schizomeria*	*Platylophus*
Vegetative characters				
Adult leaves	unifoliolate	unifoliolate or trifoliolate	simple	trifoliolate or unifoliolate
Adult leaflet form	entire or lobed	entire	entire	entire or lobed
Adaxial stipule colleters	present	present	present	present
Areolation	incomplete	well developed	well developed	imperfect
Fimbrial vein	incomplete	well developed	well developed	well developed
Veinlet sheathing	sclerenchymatous	sclerenchymatous	sclerenchymatous	parenchymatous
Terminal idioblasts	present, rare	present, rare	absent	present, rare
Hydathodes	present	present	present	present
Subsidiary cell arrangement	brachyparacytic	brachyparacytic	weakly brachyparacytic	brachyparacytic
T-piece at stomatal pole	present	present	present	present
Reproductive characters				
Inflorescence position	axillary	axillary or terminal	axillary, terminal or false terminal	axillary

Inflorescence type	solitary or cyme	cyme	cyme	cyme
Calyx aestivation	valvate	valvate	valvate	valvate
Sepal number	4	4-6	4-6	4
Petals	notched/fringed	notched/fringed or absent	notched/fringed	notched/fringed
distal connective	strongly developed	strong to weakly	weakly present	weakly present
connective protrusion		present		
on anther				
Ovary position	hypogyny	slight epigyny	hypogyny	hypogyny
Nectary disk	annular	annular	segmented	annular
Fruit morphology	septicidal capsule	indehiscent 'capsule'	drupe	imperfectly dehiscent capsule
Seed surface	reticulate	striate	striate	reticulate
Pollen apertures	2	2	2	2
Tectum	partial, discontinuous heterogeneous reticulate	partial, discontinuous heterogeneous reticulate	partial, discontinuous heterogeneous reticulate	partial, discontinuous heterogeneous reticulate
Wood characters				
Vessel distribution	solitary, radial multiples	solitary, radial multiples	solitary, radial multiples	solitary, radial multiples
Vessel perforations	simple and scalariform	predominantly simple	predominantly simple	simple and scalariform
Inter-vessel pitting	scalariform to opposite	scalariform to opposite	transitional to opposite to alternate	scalariform to opposite
Rays	weakly heterogeneous	weakly heterogeneous	weakly heterogeneous	weakly heterogeneous



Figs 34-38

Phylogenetics and Classification of Cunoniaceae (Oxalidales) Using Chloroplast DNA Sequences and Morphology

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A well supported phylogenetic hypothesis of the flowering plant family Cunoniaceae and related taxa is presented. A parsimony cladistic analysis of chloroplast DNA sequences from two loci, trnL-trnF and rbcL, and morphology show that three genera often placed in their own family, Bauera, Davidsonia and Eucryphia, are nested within Cunoniaceae. Brunellia may be most closely related to the Australian pitcher plant Cephalotus, and Aphanopetalum is in Saxifragales. Within Cunoniaceae, the New Guinean-South Pacific genera Acsmithia and Spiraeanthemum form a sister clade to the rest of family. Within this larger clade is a basal grade in which flowers mature centrifugally on an inflorescence axis, and a clade in which flowers mature synchronously to acropetally on an inflorescence axis. Other conspicuous morphological characters, including stipule position, inflorescence form, petal presence or absence, number of pollen colpi, carpel number, and fruit morphology, are homoplasious among and within clades at the tribal level. The results are used to propose a circumscription of the family, with 26 genera and approximately 300 species. Twenty genera are placed among six tribes, Cunonieae, Codieae, Geissoieae, **Caldcluvieae**, **Schizomerieae**, and Spiraeanthemeae, and six poorly resolved genera are not placed into any formally named group. Among outgroups, the Australian endemic family Tremandraceae is nested within Elaeocarpaceae.

Large-scale cladistic analyses of flowering plant DNA sequences have revealed an unexpected group of "rosid" taxa now called Oxalidales (APG 1998). This order comprises nine families recognized by Cronquist (1981), primarily from his Rosales (Baueraceae, Brunelliaceae, Cephalotaceae, Connaraceae, Cunoniaceae, and Eucryphiaceae), but also from his Polygalales (Tremandraceae), Geraniales (Oxalidaceae), and Malvales (Elaeocarpaceae).

Cunoniaceae, which may be the most diverse family of Oxalidales, is the focus of this paper, but the inclusion of several outgroup taxa provides some insight into intraordinal relationships. Our general goals are to circumscribe monophyletic taxa at the ranks of family, tribe and genus, based on cladistic analyses of DNA sequences from two chloroplast loci, the trnL-trnF intron and spacer and the rbcL gene, and of morphological and anatomical features. We are also fortunate to draw upon a wealth of data and hypotheses from previous specialists in the family, most notably the anatomist and morphologist William Dickison and the late taxonomist Ruurd Hoogland.

Based on the results presented below, we now consider Cunoniaceae to comprise 26 genera and about 300 species. They include trees and shrubs inhabiting tropical montane and lowland forests of the Americas, Malesia, islands of the western Indian Ocean, Australia, and the South Pacific, and temperate moist forests and subalpine scrub of Chile, Argentina, South Africa, Australia and New Zealand. Circumscription of the family has varied, both with respect to which genera are included and which are accepted as monophyletic. At one extreme, up to 28 genera may be included if Bauera, Eucryphia, Davidsonia, Brunellia, and Aphanopetalum are part of the family. Excluding the former genera and accepting both Hoogland's (1979) broad circumscription of Caldcluvia, and Hufford and Dickison's (1992) proposed circumscriptions of Geissois and Codia would reduce the family to 17 genera.

TrnL-F sequences of Aphanopetalum could not be aligned with other taxa in the data set, and a GenBank BLAST search suggested affinities with Saxifragaceae. A position within Saxifragales has subsequently been confirmed with other loci (M. Fishbein and D. Soltis, pers. comm.). Dickison (1994) argued for the placement of Aphanopetalum in or near

Saxifragaceae based on anatomical studies. Aphanopetalum is therefore excluded from Cunoniaceae and not part of our phylogenetic analyses.

Within-family phylogenetic relationships have been poorly known. Engler (1928) proposed the most recent intrafamilial classification, but his groups are almost certainly artificial. Previous cladistic analyses of the family by Hufford and Dickison (1992, abbreviated H&D) and Orozco (1997) were based solely on anatomical and morphological data, giving clades only weak to moderate support. Here, we intend to discover well supported clades and reclassify Cunoniaceae. A strong phylogenetic hypothesis will also allow us to evaluate ideas about character evolution and biogeography.

Biogeographic Hypotheses. Molecular systematics will be used to test hypotheses of cladistic-area relationships based on morphology. This analysis can address questions at a broad geographic scale to learn how taxa from the Americas and South Africa, which have few genera, relate to the rest of the family. Without exception, an American or South African genus does not appear closely related to a sympatric genus, but to groups from eastern Australia, eastern Malesia and the South Pacific (i.e. Australasia-Pacific), where most cunon genera occur. The overall geographic pattern is that putatively related but morphologically divergent taxa occur on disjunct, Gondwanan continents, suggesting that current distributions reflect continental vicariance rather than recurrent or recent dispersal, and that the family was diverse and widespread on Gondwanaland prior to its breakup (as suggested by Raven and Axelrod 1974). If this is true, molecular data should confirm the following hypothesis of relationships.

- The South African endemic genus Platylophus is related to Schizomeria, Ceratopetalum and Anodopetalum from Australia and Malesia. These genera share small, apically incised petals, indehiscent fruits (except Anodopetalum, Barnes and Rozefelds 2000), and thyrsoid to cymiform inflorescences. In H&D (1992) these genera were part of the same clade, but this clade was not fully resolved in the strict consensus tree.
- Cunonia capensis L. from South Africa is related to all other Cunonia from New Caledonia. Species of Cunonia share a unique,

circumbasal-acropetal dehiscence of the fruit (Hoogland et al. 1997; Bradford 1998), but the outlying distribution of C. capensis and its divergent exine structure (Hideux and Ferguson 1976) has led to some question of the monophyly of Cunonia (e.g. Cronquist 1981).

- Caldcluvia s.s.(sensu stricto) from South America is related to Ackama, Spiraeopsis and Opocunonia from Australia, Malesia and New Zealand. All these genera share abaxial tuft domatia on leaves, and Ackama, Spiraeopsis and Opocunonia share dichogamous sexual expression (Hopkins in prep.). This group was first proposed by Hoogland (1979), who reduced all these genera into Caldcluvia s.l. (sensu lato). However, he did not indicate any character that could be interpreted as a synapomorphy for this group, and others have not accepted it based on the diversity of its fruit morphology (Godley 1983), seed morphology (Webb and Simpson 1991), and vegetative anatomy (Dickison 1980). Pollen is also distinct among the genera (Hideux and Ferguson 1976). Not surprisingly then, in Hufford and Dickison's (1992) cladograms Caldcluvia s.l. is polyphyletic. However, the domatium character has never been evaluated cladistically and may be the only known derived feature that unites the group.
- Lamanonia from South America is related to Pseudoweinmannia and Geissois from Australia and the South Pacific. These genera share palmately-compound leaves, a racemose flower-bearing axis, a single perianth whorl, and a polystemonous androecium. This relationship is widely accepted, and H&D (1992) even suggested that Lamanonia and Geissois be combined. However, Geissois may be more closely related to Pseudoweinmannia than to Lamanonia.
- Brunellia from South America is related to Acsmithia and Spiraeanthemum from the Malesian-Pacific region. These genera share a single perianth whorl; a gynoecium of usually more than two, free carpels; carpels vascularized by three ventral vascular bundles; biovulate carpels; non-inrolled carpel margins; and epitropous micropyles (Eyde 1970; Dickison 1975c). Brunellia has

traditionally been placed in its own family and considered closely allied with the Cunoniaceae (Cuatrecasas 1970). Like the Cunoniaceae in general, it has decussate, toothed leaves and interpetiolar stipules. Orozco (1997) suggested including Acsmithia and Spiraeanthemum in an expanded Brunelliaceae. In H&D (1992), Brunellia was part of a clade with Acsmithia, Spiraeanthemum, Gillbeea and Aistopetalum, all genera with more than two carpels. But carpels are fused and fruits are indehiscent in Gillbeea and Aistopetalum, whereas in Brunellia, Acsmithia and Spiraeanthemum carpels are free and fruits are follicular. One of the putative outgroups, Cephalotus, has floral and fruit morphology similar to Brunellia.

In addition to Cunonia, two other genera, Eucryphia and Weinmannia, are disjunct across the southern hemisphere. Eucryphia occurs in Chile, Argentina and Australia, but the monophyly of the genus is nearly certain (Taylor and Hill 1996; Forster and Hyland 1997). Weinmannia constitutes about one half of the species in Cunoniaceae and is widely distributed in the tropics. The monophyly of Weinmannia was weakly supported by a morphological cladistic analysis (Bradford 1998). The monophyly of each Weinmannia section is better supported, and one of them, Weinmannia section Weinmannia is disjunct between the Americas and the Mascarene Islands (W. Indian Ocean). A molecular systematic analysis of Weinmannia and its relatives (Bradford unpubl. data) will be reported elsewhere.

Morphological Hypotheses. Hypotheses of character evolution from H&D (1992) can be reevaluated with a molecular-based phylogeny. For example, taxa with more than two carpels may form a basal grade, and a bicarpellate gynoecium is a potential synapomorphy of a large clade. H&D (1992) also suggest that Engler's (1928) tribe Pancherieae, which unites Pancheria, Codia and Callicoma on the basis of their spherical-head (i.e. capitate) inflorescence form, is polyphyletic. However, H&D (1992) suggested combining Pullea (in tribe Pulleae sensu Engler) and Codia based on anatomical similarities, and two species of Pullea do have strongly aggregated flowers, although P. glabra often does not. Although flower-bearing axes may be homologous in Pullea and Codia, the spatial

arrangement of those axes (i.e. the inflorescence architecture) in Pullea is unique in the family and supports the distinction of the genus (Appendix 1). Therefore, based on H&D's (1992) cladograms and our exclusion of Pullea from Codia, capitate inflorescences may have four unique origins in Cunoniaceae.

Our morphological data matrix includes an inflorescence character not previously discussed in Cunoniaceae, whether flowers mature synchronously to slightly acropetally versus centrifugally on the flower-bearing axis (see Appendix 3). The two states differ among roughly half the genera, making the character a potential synapomorphy for a large clade.

Cunoniaceae have diverse fruit morphology (Dickison 1984). Most genera have dry, dehiscent fruits (capsular or follicular), and this is probably the plesiomorphic condition. Several taxa have indehiscent fruits of various forms, and the phylogeny can be used to infer the number of times indehiscence has evolved. Although they look similar, the densely pubescent ovaries of Codia and Pseudoweinmannia (hairy nuts), and the half inferior ovary and expanded sepals in Pullea and Ceratopetalum (pseudosamaras) are probably convergent structures. Fruits in Platylophus are bladder-like indehiscent capsules (utricles). Gillbeea, with dry, lateral outgrowths of the carpel wall, and Aistopetalum, with drupaceous fruits, were closely related in the cladograms of H&D (1992). The relationship of Davidsonia, with soft drupaceous fruits, to other cunons has not previously been investigated cladistically.

MATERIALS and METHODS

Choosing Terminal Taxa. With a large group like Cunoniaceae, an initial survey of morphological diversity helps appropriately sample and circumscribe taxa for cladistics, especially when using molecular exemplars. Plausibly monophyletic terminal taxa, corresponding as much as possible to traditional generic boundaries, were sought using morphological characters. Most genera are probably monophyletic, and Appendix 1 gives the characters supporting the monophyly of each Evolutionary Unit (EU) in the analysis.

Weinmannia, Cunonia and Geissois are among the most species-rich and diverse genera in the family. They were split into putatively monophyletic EUs to reflect this diversity, avoid possibly paraphyletic groups, and test for the monophyly of these genera. The DNA data set complements the morphological one by sampling, where possible, one or more species from each EU for DNA sequencing. Fresh or silica-gel dried leaf material was unavailable for only Aistopetalum, Opocunonia and Lamanonia, and attempts to extract DNA from herbarium specimens failed.

Morphological Characters. Morphological characters were in most cases examined before molecular ones. There is probably the tendency when building data matrices to ignore characters that do not conform to already held beliefs about relationships. In this study system, our notions of which genera might be closely related were largely based on H&D (1992), the taxonomies of Hoogland (1960; 1979; 1981) and our own experience. However, none of these previous studies strongly indicated deep-level phylogenetic relationships among groups of genera, and our own minds could not contrive a convincing phylogenetic scheme of the family.

Perhaps because of our ignorance of the major structure of Cunoniaceae phylogeny, we included vegetative and reproductive characters liberally, even while accumulating molecular data began to suggest they were homoplasious. Scored polymorphisms were usually among species within a genus rather than within species. However, most genera lack detailed taxonomic descriptions or recent monographs, and we may have overlooked variation within genera. Missed variation is most likely with anatomical or micromorphological characters that are sampled less intensively. However, for most characters we delimited in this data set, little or no variation was found within specimens, within species, or between species of the same genus or EU. Only 4% of the cells (78 of 1,872) in the data matrix are scored as polymorphic, and of these, 21% (16 cells) are from the three most species-rich genera, suggesting that their variation has been sampled broadly.

The majority of morphological characters in our data set are visible on herbarium specimens using the naked eye or a dissecting microscope. Most characters have been previously illustrated or documented photographically (but not necessarily for all EUs) in

taxonomic treatments or anatomical surveys (see references in Appendix 2), although these were not generally relied on for scoring of character states. Macro-morphological characters were initially compiled by J. Bradford. Specimens were examined of nearly all species of Cunoniaceae from collections in these herbaria: MO, NSW, BRI and P. Live plants were studied both in natural populations and living collections (especially at University of Tasmania). One to several specimens per species were studied, with species endemic to New Guinea being least well represented among the collections examined. Hand sketches and notes were made of vegetative, floral, fruit and inflorescence features, and these were often reexamined and compared as the study progressed and the data matrix was refined.

R. Barnes either confirmed or corrected the characters scored by J. Bradford, and also added most micro-morphological and anatomical characters. Cunoniaceae genera are generally species-poor, which allows for fairly thorough sampling of micromorphology. (The most species-rich Cunoniaceae genera are: Weinmannia, ca. 150 species, Pancheria, ca. 30 species, Cunonia, 24 species, and Geissois, 20 species). For larger genera, a set of species was sampled from across the geographical and known morphological range of the genus whenever possible. All species were examined within a few genera with a modest number of species (e.g. Ceratopetalum, 8 species). Within each species studied, one to a few parts (e.g. leaves) were removed from one to few individual specimens. See Barnes (1999) for study methods, voucher information, and photographic documentation for some micromorphological features, with others to be published elsewhere.

A few anatomical characters from the data set of H&D (1992) were adapted to this study, and they were confirmed by checking the primary literature or through direct observation. Coding for Brunellia drew extensively from monographic treatments (Cuatrecasas 1970; 1985), as did scoring for outgroup genera (Smith 1953; Smith 1954; Thompson 1976; Coode 1978; Coode 1987; Bricker 1991). However, specimens of outgroup taxa were checked to confirm character states, with established classifications used to subsample within large genera such as Sloanea and Elaeocarpus.

Helen Fortune Hopkins carefully checked many morphological characters for groups from the Malesian-Pacific region with which she is familiar. Her comments on an early draft helped us clarify and describe characters states. She also questioned whether a few characters were truly discrete (e.g. Form of nectary) or if we know enough about some to code them properly (e.g. Androecial series). Ideally, we would know the genetic and developmental basis of morphological traits, and could document all our observations for peer scrutiny (see comments of Stevens 1996). The best we can offer at this time are our hypotheses of primary homology and references to the primary literature. We expect our characters will be tested and refined, both by congruence with other data in this and future analyses, and by more detailed (e.g. monographic, developmental) studies.

The morphological data set includes 39 EUs and 48 characters for a total of 1,872 cells in the matrix. Data are missing for only 19 cells, which are almost exclusively from outgroup taxa. Partitioning of inapplicable variation in the data matrix follows conventional methods as discussed by Hawkins et al (1997) and used in (Bradford 1998). Morphological and anatomical characters are described in Appendix 2, and the taxon by character matrix is given in Appendix 3.

Molecular Characters. Collections were made from native populations and botanical gardens between 1995 and 1998. Fresh leaves were dried in silica gel for eventual DNA extraction. DNA samples are vouchered by an herbarium specimen deposited at MO and the country of origin. See Appendix 4 for source and voucher information of each sequence (GenBank) and the NEXUS file used in the analysis (TreeBASE).

Molecular systematic work was done by J. Bradford in the laboratories of B.A. Schaal at Washington University in St. Louis and E.A. Kellogg at the University of Missouri-St. Louis. To extract DNA, dry leaves and sterile sand were placed in 1.5 mL microcentrifuge tubes and pulverized to a powder. QIAGEN's AP1 buffer was added to the tubes, and QIAGEN's DNeasy Plant Mini Kits were used to isolate and purify the DNA. The manufacturer's instructions (QIAGEN 1996) were modified by increasing the amount of buffers AP1 and AP2 by 20 percent.

Chloroplast loci were chosen primarily to provide resolution within Cunoniaceae and determine which genera should be included in the family;

a second goal was to understand how Cunoniaceae relates to other members of Oxalidales. The noncoding region trnL-trnF (Taberlet et al. 1991) was chosen because it was highly variable among genera, whereas the protein coding locus, rbcL, had much less variation among genera but could be aligned and compared with a diversity of outgroups, many of which had available sequences.

Standard PCR techniques were used to amplify loci. Reaction sizes ranged from 20-50-µL and each reaction contained 10 mM Tris-HCL (pH 9.0), 50 mM KCl, 2.5 mM $MgCl_2$, 0.1% Triton X-100, 2 units Taq Polymerase, 200 µM each dNTP, 0.2 µM each primer, and ~10-20 ng genomic DNA.

rbcL METHODS. One pair of primers for the rbcL locus ("rbcL5'FOR" and "rbcL-extREV") was designed from known sequences in Zea, Rheum and Spinacia (R. Jansen pers. comm., McIntosh et al. 1980). Amplification of the rbcL gene was done with this pair of primers, or "rbcL5'FOR" in combination with "rbcL3'REV" was used if the former combination did not amplify (see Table 1). The primer "rbcL3'REV" and two internal primers used only for sequencing, rbcL-intFOR and rbcL-intREV, were designed from published rbcL sequences of Oxalidales taxa. The following cycling conditions were used to amplify rbcL: 94°C (2 min), then 35 cycles of 94°C (30 seconds), 51°C (50 seconds), 72°C (50 seconds); and finally 72°C (3 min). A single PCR product from each reaction was purified with QIAGEN's QIAquick PCR Purification Kit. Sequencing reactions used a commercial premix and followed the manufacturers instructions (Perkin Elmer, Norwalk, CT). Reactions were loaded onto a Perkin Elmer ABI 377 automated sequencer and the lanes were analyzed by the program Sequencing Analysis (Perkin Elmer).

The program Sequencher (version 3.1; GeneCodes Corp., Ann Arbor, MI) was used to align fragments and verify sequences. Twelve additional rbcL sequences were acquired for this study from GenBank, and one unpublished sequence was kindly provided by D. Soltis. All sequences were aligned by eye in Se-Al (Rambaut 1995) and were further verified by studying amino acid translations and comparing these to known site variation and constraints (Kellogg and Juliana 1997). This identified likely errors for three taxa, Aceratium ferrugineum, Davidsonia pruriens

and Elaeocarpus grandis, with each error corresponding to an amino acid change in a conserved, active site. The single Aceratium sequence error was at amino acid position 66, corresponding to nucleotide C instead of a G at position 198. The Davidsonia sequence (done manually, D. Soltis, pers. comm.) had two apparent errors affecting amino acid positions 45, 337 and 338. The nucleotide sequence at positions 134-135 was given as "TT" instead of "AA" and the sequence at positions 1009-1012 was given as "CCCC" instead of "GGGG". Each nucleotide position judged to be incorrect was replaced with an "N" prior to phylogenetic analysis. The sequence of Elaeocarpus grandis was not used in the analysis due to a number of probable errors. Also, the sequence of Averrohoa was not used in final analyses because it differed dramatically from all other sequences. For example, the most parsimonious trees without Averrohoa have a length of 431, whereas those with Averrohoa included have a length of 533, although the topology within Cunoniaceae is unaffected. Future analyses should sample broadly within Oxalidaceae and resequence Averrohoa.

TRNL-TRNF METHODS. Primers c and d, and e and f, designed by Taberlet et. al (1991), were used to amplify the intron in the chloroplast gene for tRNA-Leu (trnL) and the intergenic spacer between trnL and the exon for tRNA-Phe (trnF) respectively. The intergenic spacer between trnT and trnL did not amplify and primers c and f did not work in combination. The following cycling conditions were used: 94°C (2 min), then 35 cycles of 94°C (30 seconds), 62°C (50 seconds), 72°C (50 seconds); and finally 72°C (3 min). A single PCR product from each reaction was purified with QIAGEN's QIAquick PCR Purification Kit. DNA sequencing used fmol (Promega) direct cycle sequencing with a (^{35}S)a-dATP label, followed by electrophoresis on a 6% Long Ranger acrylamide gel (FMC), blotting and drying onto paper, and exposure to x-ray film. Forward and reverse primers were used to sequence each strand of DNA, which generated substantial areas of overlap. Sequences from primers d and e were electrophoresed for both 3 and 7 hours, whereas sequences from primers c and f were usually electrophoresed for 3 hours. However,

sequences of primer f were often poor, and therefore most of the data for the trnL-trnF intergenic spacer is based on primer e sequences.

Sequences were aligned by eye in Se-Al (Rambaut 1995) and exported in a NEXUS format for phylogenetic analysis. Both the intron and spacer region had numerous indels, some in the intergenic spacer being very large (see Discussion). Indels were scored in a character by taxon matrix in MacClade (Maddison and Maddison 1992), with each "character" corresponding to an aligned position and with all indels weighted equally. An exclusion set of characters was created in PAUP (Swofford 1999) for regions of the sequences judged to be independently evolved insertions (i.e. insertions with very different base composition and/or length). Therefore, some indel sites were treated as multistate characters, although most indels were either present or absent.

The trnL intron sequences analyzed here begin near the 5′ end of the intron and end at the start of the 3′ exon, corresponding to positions 149 through 622 of the trnS-trnF sequence in tobacco (Yamada et al. 1986). The trnL-trnF spacer sequences begin near the 5′ end of the spacer and end at the start of the exon, corresponding to positions 691 through 1029 in tobacco. In several species the 5′ end of the trnF gene was sequenced, but this was not used in the analysis.

Phylogenetic Analyses. Parsimony cladistic analyses used PAUP*4.0b2a (Swofford 1999) run on an iMac computer. The three data sets differed in size and resolution, making it necessary to analyze each somewhat differently. The analyses of each data set is described below: A, rbcL alone; B, trnL-F alone; C, combined chloroplast; and C, morphology and anatomy. For all analyses the following options were used: characters unweighted and unordered (except for one ordered morphological character), searches heuristic, starting trees obtained via random stepwise addition, TBR branch swapping, COLLAPSE option on, STEEPEST DESCENT option off, MULTREES on.

A. Oxalidales has no known sister group, being part of an ordinal-level polytomy within the "eurosids I" clade (APG 1998). Without a useful outgroup, trees needed to be rooted internally. Although the rbcL data set did not have enough congruent variation to swap to completion in a parsimony analysis, several searches were run, with each run terminated

after over 1000 to over 30,000 most parsimonious trees with a length of 431 had been found. Each replicate was rooted with the "Midpoint rooting" (minimum F-value) option in PAUP and each gave an identical strict consensus tree. A bootstrap analysis of the rbcL data was done using 10,000 replicates of the "Fast" stepwise-addition search option.

B. The trnL-trnF data set was first analyzed using 100 heuristic search replicates with TBR branch swapping. Next, 1000 bootstrap replicates with TBR branch swapping and MAXTREES set at 100 per replicate were done. Trees were rooted with the assumptions that Brunellia is more closely related to Cunoniaceae than to Elaeocarpaceae and Tremandraceae, and that together Elaeocarpaceae and Tremandraceae form a monophyletic group. These relationships are compatible with, but not well supported by, the rbcL data and are suggested by morphological data (see Discussion).

The contribution of insertions and deletions to cladistic resolution and support was also studied. Following the search protocols used with all characters included, a parsimony and bootstrap analysis of the trnL-trnF data set excluded all indel characters. A third parsimony analysis excluded "small" indels, which were defined as those only 1-2 bp long or length variations in regions that repeated the same nucleotide (e.g. strings of As or Ts).

C. A combined analysis of chloroplast DNA sequences followed the methods outlined for the trnL-trnF data set although the MAXTREES setting was not limited during bootstrapping. A decay index for each clade was also done for the combined chloroplast data by (1) finding the strict consensus of trees one to five steps longer than shortest trees, and for clades with decay values of six or greater, (2) finding the shortest length of trees incompatible with the constraint tree of a clade. The combined data set used identical exemplars for all species except: Bauera rubioides, Ceratopetalum gummiferum, and Davidsonia pruriens (see Appendix 4). Cephalotus sequences came from different labs, but used the same collection.

D. The morphological (including anatomical) data set was analyzed in three ways. The first was an unconstrained parsimony analysis. Because this failed to resolve many clades, the second analysis used a

constraint tree built in MacClade (Maddison and Maddison 1992) based on strongly to moderately well supported clades found by the molecular analyses. This analysis of the morphological data accepted only the most parsimonious trees congruent with the topology of the constraint tree. Multiple heuristic searches used TBR branch swapping.

A third morphological analysis was done to resolve relationships among tribes and unplaced genera by using a subset of characters that were chosen as follows. (1) The support given certain clades by molecular characters showed that some morphological characters were very homoplasious among tribes while others were relatively conserved. (2) Given the supposition that these conservative characters could resolve intertribal relationships more reliably than the more homoplasious ones, a subset of less homoplasious characters was chosen. (3) A subset of 14 characters was chosen with each character varying primarily among the tribes or unplaced genera and with an RI of 0.5 or greater from the second analysis (Fig. 4). (4) A parsimony analysis of the selected characters enforced topological constraints similar to those in the second analysis, and with the added constraint that the tribes be monophyletic. This could be viewed as a kind of successive weighting procedure by using an RI criterion for selecting characters. However, the more important criterion is that selected characters vary between tribes and are mostly constant within tribes. This set of characters is needed for a phylogenetic analysis at this level, and we are primarily using the knowledge gained from molecular analyses to circumscribe tribes and reselect morphological characters with appropriate variation. Characters that varied often within tribes would not meet the RI criterion anyway, but a few of the chosen characters do vary within a tribe. The 14 selected characters are set in bold in Appendix 2.

RESULTS

rbcL Results. The data set contained 37 EUs and 1430 characters of which 121 were informative. Nucleotide variation was low (p values ranged from 0.002-0.032 within Cunoniaceae to 0.068 overall). The most parsimonious trees had a length of 431 (CI=0.68, RI=0.68), and midpoint rooting suggests that Oxalidaceae and Connaraceae form a sister clade to the rest of the taxa (Fig 1). This agrees with previous findings in larger analyses (e.g. Chase et al. 1993; Morgan and Soltis 1993; Price

and Palmer 1993; Morgan et al. 1994; Garnock-Jones et al. 1996; Soltis and Soltis 1997; Källersjö et al. 1998; Thulin et al. 1998). Relationships among the remaining families are not resolved, although Platytheca (Tremandraceae) is nested within an Elaeocarpaceae clade. Two genera of Elaeocarpaceae, Aristotelia and Sloanea, are unresolved.

Cunoniaceae are weakly supported as monophyletic in the Fast-bootstrap analysis, with Acsmithia and Spiraeanthemum forming a sister group to a clade of all other genera. Most Cunoniaceae are in a well supported clade, but with little internal resolution. As expected, the monophyly of Eucryphia (using E. cordifolia from Chile and E. lucida from Australia) is supported, and a clade is formed by Geissois benthamii and Pseudoweinmannia lacnocarpa from Australia. Caldcluvia s.l. is also monophyletic, but Opocunonia was unavailable for analysis. Bauera is found in a clade with Davidsonia, Ceratopetalum, Platylophus and Anodopetalum, although the support for this group is not strong. The position of several other genera is unresolved.

About two thirds of cunon species are in Weinmannia, Pancheria and Cunonia, and members of these genera form a clade, although the position of a species from Weinmannia section Weinmannia is unresolved. Also placed in this clade is a sequence from a plant (called 'X-it') found in montane New Zealand. This stunted shrub has no known flowers, and was previously identified as belonging to Cunoniaceae based on its rbcL sequence (Garnock-Jones et al. 1996). With denser taxon sampling, this analysis suggests the plant is a Weinmannia species from section Leiospermum, being in a clade with W. raiatensis from the Society Islands. Most likely, it is closely related to, or conspecific with, W. racemosa, which is common at lower elevations near where the unidentified plant was found. Unpublished morphological, anatomical and cytological data also support a close relationship with Weinmannia (Garnock-Jones et al. 1996), including multicellular hair bases that are considered autapomorphic for the genus (see Appendix 1).

trnL-trnF Results. With all data included (analysis 1) there were 52 EUs and 995 characters of which 203 were informative. Nucleotide variation in trnL-trnF was much higher than in rbcL (p values ranged from

zero to 0.086 within family to 0.11 overall). The analysis found 13,080 most parsimonious trees of length 601 (CI=0.73, RI=0.80). The strict consensus and bootstrap analyses produced trees with identical topologies (Fig. 2). Of 34 resolved nodes, 18 are strongly supported (bootstrap ≥90%), 10 have moderate support (bootstrap 70-89%), and 6 have low support (bootstrap 50-69%). The strongly supported clades tend to be terminal groups of taxa, whereas internal nodes generally have moderate to weak support. One exception to this is the node supporting the monophyly of Cunoniaceae with a bootstrap value of 93%. Most areas of polytomy occur among closely related taxa, such as within and among sections of Weinmannia and the genera of Caldcluvia s.l. Another major polytomy is among groups in a large clade that shares a 33 bp deletion in the spacer region (i.e. the clade labeled "Small Deletion/Core Cunon" in Fig. 2).

With indels excluded (analysis 2) there were 955 characters, of which 163 were informative. The analysis found 216 most parsimonious trees with length 480 (CI=0.75, RI=0.80). There was better resolution in the Small Deletion/Core Cunon clade than analysis 1 (Fig. 2). Four clades not found in the strict consensus tree of analysis 1 were resolved in analysis 2, conversely, two clades resolved in analysis 1 were not resolved in analysis 2. Although the strict consensus tree was more resolved in analysis 2, fewer clades had strong bootstrap support and bootstrap values were generally lower than in analysis 1. Of thirty clades found in the bootstrap analysis, 14 were strongly supported, 10 clades had moderate support, and 6 had low support.

Small indels accounted for 16 of the 40 total indel characters. Excluding only small indels (analysis 3) produced 72 trees of 529 steps, and a strict consensus tree identical to that found for analysis 2. A bootstrap analysis excluding small indels gave results similar to analysis 1. Only one clade in analysis 3 had a bootstrap value differing by more than 5% from analysis 1 (Fig. 2).

The trnL-F analyses found many of the same groups as did the rbcL analysis, but with more complete taxon sampling and generally higher bootstrap values. Resolution among clades is improved, notably a clade easily recognized by a 111 base pair deletion in the spacer region and including the genera Vesselowskya, Pancheria, Cunonia and Weinmannia

(called the "Big Deletion" clade). The genera Callicoma and Codia are resolved as sister taxa and, along with Pullea, are part of clade that includes the Big Deletion clade. Fifteen genera share a 33bp spacer deletion (called the "Small Deletion/Core Cunon" clade) and this clade includes the Big Deletion clade and its close relatives, Caldcluvia s.l., the Geissois clade, Acrophyllum, Gillbeea, and Eucryphia.

Four genera, Schizomeria, Platylophus, Ceratopetalum and Anodopetalum comprise a well supported clade (labeled "Schizomeria clade" in Fig. 2) with Schizomeria sister to the rest. The Schizomeria clade is a sister group to the Core Cunon clade. In contrast to the results of the rbcL analysis, Davidsonia and Bauera are not grouped with genera of the Schizomeria clade, but instead form a basal grade, with the Acsmithia+Spiraeanthemum clade still resolved as the sister group to the rest of the family.

Among outgroups, Tetratheca (Tremandraceae) is nested within Elaeocarpaceae near Elaeocarpus, which is the same position found for Platytheca (Tremandraceae) in the rbcL analysis (Fig. 1). When trees are rooted with Elaeocarpaceae as a monophyletic outgroup, Cephalotus and Brunellia are placed as sister taxa.

Combined trnL-trnF/rbcL Results. The data set had 30 EUs and 2425 characters of which 208 were informative. Twelve most parsimonious trees with 753 steps (CI=0.75, RI=0.70) were found. A phylogram of one of the trees is given in Fig. 3 (character optimization ACCTRAN), with bootstrap and decay values also shown. Bootstrap values are generally higher in the combined analysis than for comparable clades in either independent analysis. Most importantly, the combined data strongly supports the monophyly of Cunoniaceae when Davidsonia, Eucryphia, and Bauera are included. Three major clades are well supported: the large sister group to Acsmithia+Spiraeanthemum, the Core Cunon clade, and the Big Deletion clade. Within the Big Deletion clade, the monotypic Vesselowskya is placed as the sister taxon to Weinmannia, Cunonia and Pancheria, with Weinmannia being paraphyletic.

The combined analysis reveals three pairs of relationships not seen in either independent analysis: Gillbeea is placed as the sister taxon

to Caldcluvia s.l.; Eucryphia and Acrophyllum are sister taxa; and the Eucryphia+Acrophyllum group is sister to the clade comprising Pullea, Callicoma+Codia and the Big Deletion group. However, none of these three relationships have strong support.

When analyzed separately, the chloroplast data sets conflict in the positions of Bauera and Davidsonia, placing them either in an unresolved polytomy with the Schizomeria clade or as part of a basal grade (Figs 1 & 2). Although Bauera and Davidsonia are shown together as a sister group to the Schizomeria clade in Fig. 3, in the strict consensus tree they are parts of an unresolved polytomy that includes the Schizomeria clade and the Core Cunon clade.

Morphological Analyses. The unconstrained morphological analysis had 39 EUs and 48 characters. Two large islands of equally parsimonious trees, each with 183 steps, were found (CI=0.36, RI=0.63). Because the islands are so large (25,000-29,000 trees), we cannot be sure all most parsimonious trees were found, however, searches did swap to completion. Clades resolved in the strict consensus of all searches are: Acsmithia+Spiraeanthemum; Schizomeria, Ceratopetalum, Platylophus and Anodopetalum; Lamanonia (Pseudoweinmannia+Geissois); Ackama+Spiraeopsis; Pullea+Callicoma, a monophyletic Weinmannia, a monophyletic Cunonia; a monophyletic Elaeocarpaceae, and a clade of Aristotelia+Tetratheca. In both islands, Gillbeea and Aistopetalum were part of the same clade, but in one set of trees these genera were grouped with Davidsonia and in the other set with Eucryphia. Those clades compatible with the molecular results are labeled in Fig. 4.

The constrained analysis with all morphological characters found 306 trees with 202 steps in two tree islands (CI=0.32, RI=0.57). Of the taxa without available DNA sequences, Opocunonia is placed within Caldcluvia s.l. as the sister taxon of Ackama and Spiraeopsis, Lamanonia is the sister group to Geissois and Pseudoweinmannia, and Aistopetalum may be related to Gillbeea and Eucryphia. Pullea is placed as the sister group to a constrained clade of Callicoma+Codia. The positions of Bauera and Davidsonia were unconstrained relative to the Core Cunon clade, the Schizomeria clade, and each other. Davidsonia is resolved as in the

trnL-F analysis, but Bauera is in a unique position as the sister group to the Core Cunon clade. The clade of Weinmannia found in the unconstrained analysis is collapsed.

The unresolved positions of Eucryphia, Aistopetalum and Gillbeea (Fig. 4) are due to conflict among the two islands of trees. One set of trees places these three genera in a clade, whereas the other island places them in a grade at the base of Geissoieae. Both islands therefore agree on a close relationship among Eucryphia, Aistopetalum and Gillbeea that is not shown by the strict consensus tree.

The constrained analysis with 14 selected characters found 151 most parsimonious trees with 73 steps (CI=0.32, RI=0.67). The strict consensus of these trees is similar to the topology of one tree island from the first constrained analysis, grouping Eucryphia, Aistopetalum, and Gillbeea in a clade that is the sister group to a clade resolved as Geissoieae (Acrophyllum (Caldcluvieae (Codieae+Cunonieae))). Figure 5 gives the inferred evolution of most of the 14 selected characters based on this analysis, although tribes are represented as a single terminal unit and variation within tribes is not shown. Intratribal relationships from this analysis are the same as shown in Fig. 4.

DISCUSSION

Taxonomic Implications.

FAMILY AND ORDINAL LEVEL. The genera Davidsonia, Bauera and Eucryphia should no longer be recognized at the family level as this would make Cunoniaceae paraphyletic (Figs 1-4). This has already been accepted by the Angiosperm Phylogeny Group (1998), which also placed Brunellia in Cunoniaceae based on the results of Hufford and Dickison (1992). However, the initial molecular systematic results show that Brunellia is most likely not part of Cunoniaceae and should be retained at the family level.

To test the position of Brunellia more rigorously, two constraint trees were built in MacClade that either forced (1) a monophyletic group of Brunellia+Cunoniaceae or (2) a monophyletic group of Brunellia (Spiraeanthemum+Acsmithia), which was the initial hypothesis of

relationships. The combined chloroplast DNA data set was used to see how many more steps would be required given the different forced topologies, and if relationships in other parts of the tree would be altered. The first analysis found 29 equally parsimonious trees placing Brunellia as a sister group to Cunoniaceae ("sister family" hypothesis), and these trees were only 3 steps longer than trees in the unconstrained analysis (756 versus 753). The second analysis found 3 equally parsimonious trees of length 761 when Brunellia is placed within tribe Spiraeanthemeae ("Spiraeanthemeae" hypothesis). One unconstrained tree was found with a topology identical to one shortest tree from each constrained analysis (except for the clades being tested). This tree was used as the "best" tree in comparisons with two constraint trees to test if the data set can reject the alternative hypotheses of the position of Brunellia.

The Wilcoxon signed-ranks test (Templeton 1983; Larson 1994; Mason-Gamer and Kellogg 1996) as implemented in PAUP*4.0b2 did not reject the sister family hypothesis (N=3, T=6, P=0.0833). The Spiraeanthemeae hypothesis was barely rejected (N=16, T=34, P=0.0455). However, the test does not account for the homoplasy of each character, which in this case strengthens rejection of the Spiraeanthemeae hypothesis. Of the twelve characters lengthened by one step by the constraint tree, eleven have an RI of 1.0 in the unconstrained tree and one has an RI of 0.5. By contrast, of the four characters shortened by the constraint tree, two remain homoplasious even on the constraint tree (RI=0.63 & 0.55).

In summary, the sister group relationship between Brunellia and Cephalotus cannot be statistically distinguished from an alternative hypothesis placing Brunellia as the sister group to Cunoniaceae. Furthermore, the rooting of the cladograms in Figs. 2 & 3 is based on outgroup assumptions that need testing in a broader context, and we would not be surprised if future studies support a sister group relationship of Cunoniaceae and Elaeocarpaceae. While Brunellia and Cephalotus do share some obvious features, such as apetalous flowers and follicular fruits of multiple carpels, these may be plesiomorphic. We can be fairly confident, however, that retaining Brunelliaceae does not make Cunoniaceae paraphyletic, while placing Brunellia in Cunoniaceae may make the family paraphyletic with respect to Cephalotus.

The family Tremandraceae is endemic to Australia with three genera. Two of these, Tetratheca and Platytheca, were included in this study and each is nested within Elaeocarpaceae in a clade with Elaeocarpus. Morphological synapomorphies for an expanded Elaeocarpaceae clade may include poricidal anthers, basifixed anthers, fused styles, loculicidally dehiscent carpels, and vessels in radial-multiples. Future studies should include Connaraceae and Oxalidaceae to better identify synapomorphies of Elaeocarpaceae.

TRIBAL AND GENERIC LEVELS. Engler's (1928) tribal classification of Cunoniaceae bears little correspondence to phylogeny. We propose a new tribal classification to circumscribe monophyletic groups of genera. Poorly resolved genera, Bauera, Davidsonia, Aistopetalum, Gillbeea, Eucryphia, and Acrophyllum, are not placed in any tribe (Fig 4). Twenty of the twenty-six genera are therefore included in six tribes: Cunonieae, Codieae, Caldcluvieae, Geissoieae, Schizomerieae, and Spiraeanthemeae. Each tribe is briefly described in Appendix 5.

Leaving genera unplaced may be unsatisfying to some taxonomists, but given our current understanding of cunon phylogeny we believe this method best serves the purpose of classification and it has precedents (e.g. Bentham and Hooker 1862-1883; APG 1998). Phylogenetic classifications communicate our knowledge of relationships, and by not including some genera in tribes we are indicating important information about lack of phylogenetic resolution. However, we do know that four unplaced genera are in the Core Cunon clade (Fig. 2), which could conceivably constitute a subfamily and communicate more information. Conflicting resolution among Bauera, Davidsonia, and Schizomerieae (Figs. 1-5) makes it difficult to confidently establish other monophyletic subfamilies besides a subfamily of tribe Spiraeanthemeae. To avoid taxonomic instability, clades above the tribal level will not be named until better resolution and support for trees are available. As unplaced genera become resolved, we will also try to ensure the stability of tribal nomenclature and to name as few monotypic tribes as possible. In the meantime, Appendix 1 lists the informal group placement of unplaced genera, which are in either the Core Cunon clade or the Basal Grade (Fig. 2).

Engler's tribe Pancherieae is no longer recognized, with its members now part of Cunonieae (Pancheria) and Codieae (Codia and Callicoma). Engler's Cunonieae, which formerly included all members of the new tribes Caldcluvieae and Schizomerieae, and Pseudoweinmannia (now in Geissoieae), is much reduced, and now includes just Cunonia, Weinmannia, Pancheria, and Vesselowskya. Engler placed all genera with more than two carpels in tribe Spiraeanthemeae, but this is a homoplasious character (Fig. 5) and Spiraeanthemeae is reduced to Acsmithia and Spiraeanthemum.

Four tribes, Spiraeanthemeae, Schizomerieae, Geissoieae and Cunonieae have strong molecular and morphological support (Figs. 3 & 4). Caldcluvieae, a tribe comprised of Hoogland's Caldcluvia s.l., has strong molecular support but only one known morphological synapomorphy (Fig. 4). From a morphological perspective, each genus is easily distinguished (Appendix 1) whereas the tribe is not.

Codieae has weak molecular support and only modest morphological support in our data set (Figs. 3 & 4). However, we did not include some apparently derived seed characters used by H&D (1992) to argue that Codia and Pullea were closely related. These seed characters include: seeds less than 1 mm long, seed surface reticulate, and seed coat thin and undifferentiated (Dickison 1984). Other possibly unifying characters include terminal idioblasts in leaf veinlets (Dickison 1975b), anomocytic subsidiary cells, supernumerary axillary buds, flowers in capitula, absence of petals, indehiscent fruits, and an epigynous perianth. Some of these presumably derived characters are either variable within Codia or Pullea, or lacking altogether in Callicoma (Appendix 3). Although individual characters may be weak, we feel that the overall congruence among them provides sufficient support for the tribe.

Two morphological characters in our data, the absence of a stylar canal and a gynoecium of three or more carpels, suggest that Aistopetalum, Gillbeea and Eucryphia may form a clade (Fig. 5). Similarities in carpel anatomy among Aistopetalum and Gillbeea were noted by (Dickison 1975c).

Within tribes Cunonieae and Geissoieae, generic circumscription needs further evaluation. The chloroplast data suggest that Weinmannia (Cunonieae) is paraphyletic (Figs. 2 & 3) whereas morphological data support its monophyly (Appendix 1; Fig. 4; Bradford 1998; Barnes, unpubl. data). More detailed molecular systematic analyses of both nuclear and chloroplast loci (Bradford, unpubl. data) are inconclusive as to whether Weinmannia is monophyletic (Bradford 1999). We therefore have little understanding of relationships within Cunonieae, although each section of Weinmannia is monophyletic (Fig. 2 and Bradford unpubl. data) and morphologically distinct (Bradford 1998).

Geissois as now circumscribed includes two distinct species-groups, one from the South Pacific (Geissois 1) and another from Australia (Geissois 2). No morphological synapomorphy is known for the genus although each species-group has clearly derived features (Appendix 1). Dickison and Rutishauser (1990) suggested that Lamanonia was nested within the two Geissois groups, whereas our analysis places Lamanonia sister to other Geissoieae and Pseudoweinmannia as the sister genus to Geissois. Although our results support the monophyly of Geissois (Figs. 2 & 4), this should be evaluated by an intratribal analysis.

Evaluating Biogeographic Hypotheses.

SOUTH AFRICAN TAXA. As expected, Platylophus is in the tribe Schizomerieae, with the rbcL data supporting a sister group relationship to Anodopetalum from Tasmania (Figs. 1 & 3). Anodopetalum and Platylophus have capsular or capsular-like fruits (indehiscent in Platylophus) and both lack a scleritized inner integument of the seed coat (Dickison 1984). The trnL-F analyses place Cunonia capensis in tribe Cunonieae, but its relationship to New Caledonian Cunonia species is unresolved (Fig. 2).

AMERICAN TAXA. Both rbcL and trnL-F analyses place Caldcluvia in a clade with Ackama and Spiraeopsis, and the constrained morphological analysis includes Opocunonia in this group, forming Caldcluvieae. Lamanonia was unavailable for molecular analysis, but the morphological analysis places it as the sister group to Geissois and Pseudoweinmannia,

forming Geissoieae. Even without molecular data, morphological and anatomical data alone strongly support the grouping of these genera (Fig 4).

Brunellia does not appear to be the sister genus to tribe Spiraeanthemeae, but rather to Cephalotus from southwestern Australia (Figs. 2 & 3). Although our initial hypothesis is rejected, the general pattern of relatedness between Australasian-Pacific and American groups is confirmed.

Morphological Evolution. The constrained analysis of all characters forces nineteen more steps than the unconstrained analysis. Although this seems like many more steps, it is only about 10% more homoplasy overall (RI-unconstrained=0.63 versus RI-constrained=0.57). Many morphological characters are more homoplasious than implied by the analysis of Hufford and Dickison (1992) and the unconstrained morphological analysis here, although a few are less homoplasious. The phylogenetic hypothesis in Fig. 5 will be emphasized to discuss character evolution.

The plesiomorphic condition for carpel number is greater than two, and a large clade can be recognized as having two carpels. But carpel number within this clade has apparently been reversed at least three times, once in Schizomeria and in Caldcluvieae, and at least once more if Eucryphia, Gillbeea and Aistopetalum are placed in a clade. The absence of a stylar canal characterized a basal grade in H&D (1992), but this analysis shows this feature to be derived in a possible Eucryphia, Gillbeea and Aistopetalum clade, and in Spiraeopsis (Caldcluvieae). Carpel similarities noted by Dickison (1975c) between Spiraeanthemeae and Brunellia (i.e. apocarpy, biovulate carpels, 'five trace' vascularization) are apparently plesiomorphic. Gynoecia in Connaraceae, for example, are similar (Dickison 1971).

We coded two inflorescence characters, the form of flower-bearing axes, and the timing of floral maturation within those axes. Inflorescence form is relatively homoplasious among tribes and unplaced genera, but fairly consistent within tribes (Fig. 4). Branched flower-bearing axes, thyrsoid to cymiform or paniculiform, are plesiomorphic. The capitate form is perhaps less homoplasious than suggested earlier,

having evolved once in Cunonieae (Pancheria) and once or twice in Codieae (Pullea is polymorphic). Racemose forms have arisen twice, as apomorphies for Cunonieae and Geissoieae. Solitary flowers are independently evolved in Eucryphia, Bauera, and in Anodopetalum, although Anodopetalum rarely has a 3-flowered cyme (Barnes and Rozefelds 2000) and was scored as cymiform in the data matrix (Appendix 3). Eucryphia flowers are subtended by a pedicel, two small bracts, and a peduncle, suggesting a reduction from compound inflorescence as in Anodopetalum. Two proposed relatives of Eucryphia, Gillbeea and Aistopetalum, have paniculiform flower-bearing axes with terminal flowers that could be reduced to a single flower. Bauera flowers are subtended only by a pedicel.

The timing of floral maturation within an axis is less homoplasious than inflorescence form, and may have changed just twice (Fig. 5). Centrifugal timing is plesiomorphic, while synchronous to acropetal timing is an apomorphy for Spiraeanthemeae, and a synapomorphy for the clade formed by Cunonieae, Codieae, Acrophyllum, Caldcluvieae, and Geissoieae.

Fruit morphology is variable and homoplasious (Fig. 5). The plesiomorphic condition is follicular fruits, with a reversal to this state in Pancheria (Cunonieae). However, while taxonomists have generally called Pancheria's fruits follicular (e.g. Brongniart and Gris 1864; Guillaumin 1948), Dickison (1984) described them as capsular. In fact, carpels in Pancheria are usually basally united, but most importantly, their ventral margins are inrolled, differing from the non-inrolled margins in Spiraeanthemeae and Brunellia (Eyde 1970; Dickison 1975c).

The uncertain placement of Davidsonia, Gillbeea and Aistopetalum makes reconstruction of other fruit characters ambiguous, but indehiscent fruits arose four to six times, with reversals to dehiscent fruits probably two or three times. Hypotheses of convergent fruit forms in Codia and Pseudoweinmannia, and in Ceratopetalum and Pullea are upheld. A relationship between Gillbeea and Aistopetalum is supported by carpel and fruit morphology, as both have more than two carpels surrounded by a

large, lobed disc, and indehiscent fruits, although fruits are drupaceous in Aistopetalum versus dry and light with three laterally expanded carpels in Gillbeea. Dickison (1975c) also noted similarities in carpel anatomy between Aistopetalum and Gillbeea: (1) both lack open ventral sutures at or slightly above the level of placentation (this anatomical feature may be related to the absence of a stylar canal), and (2) both have carpels with ventral bundles that lie in the septa between adjacent carpels.

In agreement with H&D (1992), polystemony has evolved three times, in Bauera, Eucryphia and Geissoieae (Fig. 5). In general, polystemony is associated with relatively large flowers for the family. Flowers are solitary and especially large and showy in Eucryphia and Bauera, unlike the usually small flowers borne in inflorescences. An enlarged floral receptacle during development may provide room for a greater number of stamens, and, in Eucryphia, perhaps carpels too.

Imbricate calyx aestivation may be a synapomorphy for Cunonieae+Codieae (Fig. 5), although valvate sepals occur in Vesselowskya and some species of Codia. Bauera and Eucryphia also have imbricate sepals.

The size of flowers, especially the sepals and floral receptacle, was not used for cladistic analysis because it is difficult to define. However, the clade formed by the tribes Caldcluvieae, Codieae and Cunonieae (Fig. 5) generally has small flower parts compared to the rest of the family (except Spiraeanthemeae).

All potential synapomorphies at deep nodes are homoplasious in more terminal parts of the tree, implying that reconstruction of ancestral states is very uncertain (see Omland 1999, for a review of assumptions and potential problems of ancestral state reconstructions). However, characters that may mark early-divergent clades are interpetiolar stipules, brachyparacytic subsidiary cells, bicarpellate ovaries and dicolporate pollen (Fig. 5). Interpetiolar stipules are a synapomorphy for Cunoniaceae, with reversal to lateral stipules having occurred perhaps four times: in Bauera, Gillbeea, Geissoieae, and Caldcluvia. Anomocytic subsidiary cells occur in most outgroups, with brachyparacytic cells being a possible synapomorphy of Cunoniaceae and typifying a large

grade of taxa (e.g. Spiraeanthemeae, Schizomerieae, Geissoieae and Caldcluvieae). Tricolporate pollen is the plesiomorphic condition with apparent early evolution to dicolporate pollen. Reversal to tricolporate pollen is a synapomorphy of Cunonieae, and has also happened within Codieae, Caldcluvieae, and Aistopetalum. Bicarpellate ovaries characterize most genera outside of Spiraeanthemeae, with possible reversal to three or more carpels in Eucryphia, Gillbeea and Aistopetalum (or a clade these genera), Schizomeria and within Caldcluvieae (Ackama and Spiraeopsis).

The ancestral state reconstruction of one wood character stood out as potentially controversial because the direction of change inferred goes against widely held views on wood evolution (e.g. Carlquist 1988, see especially Chapter 11).

Wood characters are diverse in the family, and have been reviewed in detail by Dickison (1980). When outgroups are used to polarize character states for vessel plate perforations, the inferred plesiomorphic state is simple perforations with scalariform perforations derived three times within Cunoniaceae (shown in Fig. 5), and with reversals to simple plates twice, once within Caldcluvieae and Codieae (not shown). An alternative polarization uses the character state of Spiraeanthemeae (scalariform) to infer the direction of change within the family. This suggests an evolutionary trend more in line with conventional thought on wood evolution, that is the unidirectional evolution of simple plates from scalariform ones. In this scenario, simple plates have arisen perhaps five times in Cunoniaceae with no reversals to scalariform ones, although scalariform plates predominate among genera.

Dickison (1980) noted that "advanced" wood anatomy (i.e. simple perforations) was more common in large trees and plants inhabiting drier, or more seasonal environments, which agrees with the observations of Carlquist (1975). The converse is also true, with scalariform plates found mainly among smaller trees and shrubs, and in plants from very mesic habitats (e.g. Weinmannia, Dickison 1977). However, many plants are not fixed for either simple or scalariform perforation plates, rather, one or the other predominates. In this study system, the

conventional view of vessel perforation plate evolution is therefore called into question by both the developmental plasticity within individual plants, and the apparent evolutionary lability in Cunoniaceae.

The orientation of ovules (epitropous versus apotropous) was not included in our data set because of sampling uncertainties and poor documentation in the primary literature. Orozco (1997), Cuatrecasas (1970) and Engler (1928) report epitropous ovules in Brunellia versus generally apotropous ovules in Cunoniaceae. However, Spiraeanthemeae (Dickison 1989) and Davidsonia (Bange 1952) have epitropous ovules too. This character, then, may give additional support to the basal positions of Spiraeanthemeae and Davidsonia (e.g. Figs. 4 & 5), but we are not certain of the distribution of this character in other taxa.

Evolution of rbcL. The majority of changes at the nucleotide level are silent. Of the 475 amino acids in the protein, 420 are constant, and only 23 amino acid changes are informative cladistically. Most amino acid substitutions are either restricted to a single EU, a small clade of EUs, or are homoplasious among EUs. An exception are changes at amino acid position 340 in the alpha-6 helix. The amino acid Glu occurs in most taxa, but Asp is found in a basal grade of the taxa Spiraeanthemeae, Davidsonia, Bauera, and Schizomerieae, and in Brunellia and Connarus. Switching between Glu and Asp at this position is common and probably has little functional effect (Kellogg and Juliana 1997).

Evolution of the trnL intron and the trnL-trnF spacer. Both the intron and the spacer region had numerous indels (Fig. 2). However, the intron had a relatively conserved length (range 469-548 bases, aligned length 624 bases) and no very large indels.

The aligned spacer length was 493 base pairs (bp), but actual length ranged from 145 bp in sequences of Ceratopetalum, Anodopetalum and Platylophus, where more than half of the 5′ end of the spacer is absent (aligned bp 1-246), to 383 bp in Sloanea, which has a large, apomorphic insertion (bp 288-320). Other large deletions occur in sequences of Davidsonia (missing bp 43-153), Bauera (bp 92-200), Brunellia colombiana (bp 193-256), and Elaeocarpus and Tetratheca (bp 92-273, 274). The Elaeocarpus sequence also has a large insertion (bp 435-472). Two large spacer deletions shared by many taxa are phylogenetically very

informative. Sequences of the Small Deletion/Core Cunon clade are missing bp 61-93, and, nested within this clade, sequences of the Large Deletion clade (tribe Cunonieae) are missing bp 225-336.

Despite numerous indels in the intron and spacer, sequences are aligned easily. Indels tend to occur in certain regions with conserved intervening areas. Also, insertions are nearly always recognizable as repeated sequences from adjacent positions.

The intron and spacer regions are about equally informative phylogenetically even though they differ in size and indel evolution. Of the 203 informative characters in the combined trnL-F region, the intron accounts for 110 characters (CI=0.73, RI=0.83) and the spacer region for 93 characters (CI=0.73, RI=0.77). Scored indels (autapomorphies ignored) are distributed nearly equally between the intron and spacer, with 19 and 21 characters respectively (CI=0.64, RI=0.82).

Homoplasy differs dramatically between the two classes of indels. Indels equal to or greater than 3 bp, or large indels, have excellent phylogenetic signal, a Consistency Index of about 0.92 and a Retention Index of about 0.96. By contrast, small indels, or those 1-2 bp long or length variants of single nucleotide repeats, have a Consistency Index of about 0.43 and a Retention Index of about 0.72. Despite the much lower CI of small indels versus large ones, the RI of small indels is similar to that of the nucleotide data and may be a better indicator of small indel contribution to clade support. Based on comparisons among the three bootstrap analyses, small indels appear to contribute significantly to support for only one clade, but they do not diminish support for any clade (Fig. 2).

Conclusions and Future Directions. Molecular systematics and carefully considered morphological data have greatly advanced our understanding of relationships in Cunoniaceae. The benefits to classification include a monophyletic and probably stable circumscription of the family. Tribal classification is based on monophyletic groups of genera, but several genera remain to be classified formally. Several newly discovered morphological characters are reported for Cunoniaceae, and for the first time morphological features are compared with appropriate outgroups. Character evolution can be interpreted with the phylogeny, and may foster future work aimed at understanding the origin

of homoplasy or the basis of homology of particular features. Inflorescence, androecial and fruit characters stand out as potentially interesting subjects for developmental or genetic work.

Relationships are still poorly understood at the ordinal level and within the Core Cunon clade, which includes most tribes and unplaced genera. Within tribes, intergeneric relationships suggested by molecular exemplars (Figs. 2 & 3) should be regarded as a first approximation, especially in Geissoieae and Caldcluvieae, where generic sampling for DNA characters is incomplete. Our data set necessarily overlooked many characters that vary only within tribes, and may have under represented some variation by incomplete sampling. Intratribal relationships will be best examined by character exploration among closely related genera. This has been done for Cunonieae to some extent (Bradford 1998) and work on Geissoieae is in progress (Hopkins, Bradford and Barnes).

Species of Eucryphia, and members of four tribes, Cunonieae, Caldcluvieae, Geissoieae and Schizomerieae, are disjunct across the southern hemisphere. Because the related taxa are morphologically divergent, we believe they represent descendants of lineages that were widespread on Gondwanaland and have subsequently differentiated in isolation following vicariance (although long distance dispersal has obviously occurred in Weinmannia, see map in Hopkins 1998). Testing this hypothesis would require estimating the ages of these lineages by calibrating rates of molecular evolution using the fossil record or known geologic events (e.g. Baum et al. 1998; Renner et al. in press).

Although the biogeographic hypotheses in this paper concerned relationships between the Americas or South Africa and the Australasian-Pacific region, disjunctions within Australiasia-Pacific could be tested similarly, and a molecular clock calibration may discriminate between vicariant and dispersal hypotheses. For example, the sister genera Codia and Callicoma are disjunct between New Caledonia and Australia, respectively; and similar disjunctions occur within the genera Acsmithia (Malesia, Australia, Fiji, New Caldedonia), Pullea (Australia, Malesia, Fiji), Ackama (Australia, New Zealand), and Geissois (Australia, Solomons, Vanuatu, Fiji, New Caledonia).

ACKNOWLEDGEMENTS

Jason Bradford's research has been supported by a U.S. National Science Foundation training grant (BIR-9256779) to Washington University; a Mellon Foundation grant to the Missouri Botanical Garden; a U.S. National Science Foundation Dissertation Improvement Grant (#57479), and a travel grant from the American Society of Plant Taxonomists. JB is grateful for the hospitality and assistance of many colleagues from institutions around the world, including: QCNE, LOJA, VEN, PORT, USZ, COL, P, UNIMAS, SAR, SAN, FRIM, SUVA, NOU, the Siosiomaga Society (W. Samoa), BSIP, BRI, NSW, AKU, MAU, TAN, and TEF. DNA sequencing could not have been done without the trust of B.A. Schaal at Washington University and E.A. Kellogg of the E. Desmond Lee and Family Laboratory of Molecular Systematics at UM-St.Louis, and the patience and kindness of J. Rauscher, K. Olsen, D. Hayworth and S. Malcomber. Richard Barnes was funded by an Australian Postgraduate Award. Both authors thank P. Berry, H.F. Hopkins, P.M. Richardson, and P. Stevens for comments on an early draft, Roy Gereau for writing the Latin descriptions, and editors of the Journal of the Arnold Arboretum for permission to republish illustrations from vol. 65: 175 (1984).

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TABLE 1. Primers used to amplify and sequence the rbcL gene.

rbcL5'FOR	5'GTCACCACAAACAGARACTAAAGC
rbcL-extREV	5'TTAGTAAAAGATTGGGCCGAG
rbcL3'REV	5'GAATTCAAATTTGATCTCCTTCC
rbcL-intFOR	5'AAGCACAGGCCGAAACRG
rbcL-intREV	5'CCACCAGACATACGTAACGC

APPENDIX 1. Morphological apomorphies of genera (and EUs) in Cunoniaceae, Brunelliaceae and Cephalotaceae. Features unique within the family are italicized, whereas homoplasious character states are not. Question marks denote uncertain autapomorphies. See Appendix 5 for a description of tribes. Genera not placed in any formal tribe are placed in either the Core Cunon clade or the Basal Grade (see Fig. 2).

Tribe Cunonieae

Weinmannia L.--Seeds with long hairs. *Multicellular hair bases* (in all sections but not in all species). See Bradford (1998) for apomorphies of the sections within Weinmannia.

Cunonia L.--*Fruit dehiscence circumbasal-acropetal*. Nectary adnate to ovary.

Cunonia 1 (includes most species in the genus, endemic to New Caledonia). Apomorphies unknown.

Cunonia 2 (includes the species C. macrophylla, C. schiziana & C. capensis, New Caledonia and South Africa). Andromonoecy.

Pancheria Brongn. & Gris--Leaves whorled. *Sepals vascularized by a single trace*. Gynoecium apocarpous. Flowers borne on capitula.

Vesselowskya Pamp.--*Perianth and androecium 3-merous*. *Dioecious with unisexual flowers lacking vestigial parts of the opposite sex*. *Female flowers with a single perianth whorl, male flowers with two perianth whorls*. Stigmas decurrent. Leaves digitate. Wind pollinated?

Tribe Codieae

Callicoma Andrews--*Diplostemony irregular*. Petals absent? Seeds lacking wings. Seed surface papillate.

Codia J.R.Forst. & G.Forst.--Fruit indehiscent with outer covering of lanate hairs. Ovary inferior? Vessel plate perforations simple. Adult leaves have entire margins.

Pullea Schltr.--Fruit indehiscent with slightly enlarged, persistent sepals. *Flower-bearing axes borne in a series from a peduncle*. Flowers sessile? Flowers protandrous? Ovary inferior?

Tribe Caldcluvieae

Ackama A.Cunn.--Pedicel absent. Round seeds with long hairs.

Spiraeopsis Miq.--Trichomes stellate. Stylar canal absent. Vessel plate perforations simple.

Opocunonia Schltr.--Stipules bilobed. Perianth 6-merous. Nectary disc annular. Seeds numerous (ca. 40 per fruit).

Caldcluvia D.Don--Unifoliolate leaves. Stipules lateral.

Tribe Geissoieae

Geissois Labill.--unknown

Geissois 1 (Pacific species)--Flowers red. Stipules axillary. Racemes usually cauliflorous.

Geissois 2 (Australian species, "Austrogeissois"?)--Foliaceous stipules overlapping across leaf axil. Inflorescence module (IM) of multiple metamers. IM in a medial position.

Lamanonia Vell.--Racemes borne in leaf axils. Androecium of usually 2-3 series of numerous stamens?

Pseudoweinmannia Engl.--Interpetiolar fusion of pairs of lateral stipules. Locules filled by extra growth of placenta in fruit. Fruits indehiscent (or tardily so?). Ovary densely covered with wavy hairs.

Tribe Schizomerieae

Anodopetalum A.Cunn. ex Endl.--Cymes usually reduced to one flower. Fruit capsular. Orthotropic axes arch over then new orthotropic axes repeat this to form thickets of stems. Thecae protruberences very large.

Ceratopetalum Sm.--Fruit nut-like with an enlarged, persistent calyx. Ovary half inferior.

Platylophus D.Don--Fruit an indehiscent, bladder-like capsule.

Schizomeria D.Don--Fruits drupaceous? Andromonoecious sexual system.

Tribe Spiraeanthemeae

Acsmithia Hoogland--Leaves whorled.

Spiraeanthemum A.Gray--Dioecious with male flowers lacking vestigial carpels. Nodes with more than one pair of axillary buds.

Core Cunon clade members

Acrophyllum Benth.--Shrubs with long, seldom branching stems. Leaves whorled. Inflorescence of small cymes borne at several nodes along the main stem, the main stem then resuming vegetative growth. Seeds unwinged. Seed surface papillate?

Gillbeea F.Muell.--Stellate trichomes restricted to inflorescence axes and flowers. Stipules lateral? Petals bifid with apical glands. Pollen syncolpate. Fruits indehiscent, with carpel walls expanding to form lateral wings. Seeds papillate.

Aistopetalum Schltr.--Petals absent? Fruit drupaceous? One ovule per carpel. Pollen tricolporate? Vessel perforations simple?

Eucryphia Cav.--Flowers solitary. Sepals imbricate; apically coherent; shed at floral maturity. Petals comparatively large. Stamens numerous, in three series. Ovary of a few to many (4-14) carpels.

Basal Grade members

Bauera Banks ex Andrews--Stems slender. Scrambling shrub. Leaves sessile. Stipules foliaceous. Flowers solitary. Number of perianth parts variable. Petals comparatively large. Stamens numerous, in three series. Nectary disc absent. Ovary half inferior. Seeds unwinged.

Davidsonia F.Muell.--Leaves spiral. Leaf rachis with irregular-sized teeth. Stipels abaxial. Trichomes rigid, cauducous, mildly urticating. Inflorescences borne from crown to base of trunk. Perianth lobes fused half their length. Fruit drupaceous? Petals absent?

Near outgroups

Brunellia Ruiz & Pavon--Seeds arillate. Seeds attached to follicle by a persistent funiculus. Stigmas decurrent. Stipule pairs small, usually divided to their bases. Petals absent?

Cephalotus Labill.--Distal part of leaves forming an insect-trapping pitcher. Spiral leaf arrangement.

APPENDIX 2. Morphological and anatomical characters used in the cladistic analysis. See Appendix 3 for character state distribution among taxa. Characters in bold were used for the second morphological analysis.

LEAF AND STEM FEATURES (Smith 1953; 1954; Cuatrecasas 1970; Dickison 1975b; Thompson 1976; Coode 1978; Dickison 1978; 1987; Steyermark 1988; Rutishauser and Dickison 1989; Dickison and Rutishauser 1990; Bricker 1991; Barnes and Hill 1999; Barnes and Rozefelds 2000)

1. Leaf arrangement (0=spiral, 1=decussate, 2=whorled). This is an ordered character since whorled leaves are a form of decussate ones.

2. Leaf form (0=imparipinnate, 1=palmately compound, 2=unifoliolate). Taxa with trifoliolate leaves (e.g. Pseudoweinmannia) were assumed to be palmately compound unless known relatives were obviously imparipinnate (e.g. some trifoliolate Weinmannia species). The number of leaflets is often variable within a mature plant or a plant's life cycle. Understory or juvenile foliage may be compound, whereas canopy and mature foliage may be unifoliolate. This is known in some species of Cunoniaceae (Bradford & Barnes, pers. obs.), as well as in Sloanea (Coode 1978). This data set codes mature foliage only since juvenile characters are not well known.

3. Adult leaf margin (0=entire, 1=toothed).

4. Marginal tooth vascularization (0=secondary, 1=tertiary). Teeth apices are either vascularized directly by the secondary vein or from a tertiary vein that originates at the sinus. In the later, the secondary vein terminates at the sinus.

5. Orbicular trichomes on leaves (0=absent, 1=present). These trichomes are large and glandular with a hair base of 3-4 small epidermal cells.

6. Stellate trichomes (0=absent, 1=present). Unicellular trichomes are clustered into groups of 4-10 on the leaf or stem surface.

7. Tuft domatia on leaves (0=absent, 1=present). Domatia are located in the angles between the midvein and secondary veins. Tuft domatia are clusters of hairs in this position.

8. Pocket domatia on leaves (0=absent, 1=present). These occur in the same location as tuft domatia (or may rarely extend onto lateral veins) and may themselves be sparsely to densely pubescent. They differ from tuft domatia by the pouch formed by an outgrowth of the leaf.

9. Epidermal glands (0=absent, 1=present). Two-celled glandular compartments occur on the surface of the leaf (these are not trichomes).

10. Small paired hairs (0=absent, 1=present). Thinly cutinised curly paired hairs occur in association with the stomata.

11. Stoma with cutin frill (0=absent, 1=present). A frill or ledge of cutin surrounds each stoma.

12. Subsidiary cell arrangement (0=anomocytic, 1=encyclocytic, 2=anisocytic, 3=brachyparacytic). Terminology for the arrangement of subsidiary cells around the guard cells follows Dilcher (1974), with modifications from Baranova (1987).

13. Leaf stipels (0=absent, 1=present). Stipels are recognized as small, lamina-like outgrowths at nodes along the leaf rachis, and can only be scored for compound leaves. When present, stipels are adaxial in all taxa except Davidsonia, which has abaxial stipels.

14. Stipules (0=present, 1=absent).

15. Stipule inception with respect to petiole (0=lateral, 1=interpetiolar, 2=axillary) (Rutishauser and Dickison 1989; Dickison and Rutishauser 1990). The character is not scored for plants with an alternate leaf arrangement since only lateral stipules are possible. Some Elaeocarpaceae vary their leaf arrangement within a branch from alternate to subopposite to opposite. Nodes with opposite leaves have been examined to score this character.

16. Stipule fusion (0=absent, 1=present). This character only applies to groups with stipules that are lateral at inception.

17. Supernumerary axillary buds (0=absent, 1=present).

REPRODUCTIVE FEATURES (Smith 1953; Smith 1954; Cuatrecasas 1970; Dickison 1975a; Dickison 1975c; Thompson 1976; Coode 1978; Dickison 1978; Kennedy and Prakash 1981; Dickison 1984; Cuatrecasas 1985; Coode 1987; Steyermark 1988; Bricker 1991; Endress and Stumpf 1991)

18. Floral maturation (0=synchronous/acropetal, 1=centrifugal/basipetal). This refers to the timing of floral maturation

within a flower-bearing axis. Centrifugal/basipetal describes axes in which the terminal or distal flowers are more mature than lateral or basal ones. This is most often associated with "cymiform" shapes, and may also occur in others. Synchronous/acropetal describes axes in which flowers are of similar developmental stage within a flower-bearing axis or slightly more mature towards the base of the axis.

19. Shape of the flower-bearing axis (0=paniculiform, 1=thyrsoid to cymiform, 2=capitate, 3=solitary flowers, 4=racemose). Thyrsoid to cymiform refers to branched inflorescences that end in much-branched axes bearing dense groups of flowers. In contrast, a paniculiform inflorescence bears flowers along axes that terminate linearly. Thyrsoid to cymiform inflorescences have an overall rounded outline, whereas paniculiform ones are more conical. Capitula are ball-like structures bearing flowers. Solitary flowers are borne in the axils between leaves and stems. Racemose axes are linear and unbranched throughout.

20. Calyx aestivation (0=valvate, 1=imbricate).

21. Petals (0=present, 1=absent).

22. Petal apex (0=entire, 1=incised).

23. Protandry (0=absent, 1=present).

24. Stamen number (0=diplostemony, 1=polystemony, 2=triplostemony). Diplostemonous and triplostemonous androecia have a definite number of stamens in relation to the number of perianth parts, whereas polystemonous androecia have a variable number of stamens although the number of perianth parts may be definite. A few Cunoniaceae species have haplostemonous androecia, but these are rare and certainly derived within a genus.

25. Androecial series (0=two, 1=one, 2=>two). This character is related to character 24 in that diplostemonous androecia are usually (but not always) in two series. The number of stamen series for polystemonous androecia is variable. This character is somewhat difficult to score without developmental studies, but we present it as a first approximation of the androecial variation in these taxa and hope more research will clarify homologies.

26. Filament attachment (0=dorsifixed, 1=basifixed).

27. Anther dehiscence (0=ventral slit, 1=poricidal).

28. Thecal connective protruberence (0=absent, 1=present). The connective between the thecae may be visible as a protrusion, however slight, or the connective is not visible and there is an indentation between the thecae.

29. Pollen colpi (0=tricolporate, 1=dicolporate, 2=syncolpate).

30. Tectum heterogeneity (0=homogeneous, 1=heterogeneous).

31. Floral nectary (0=absent, 1=present).

32. Nectary form (0=annular, 1=segmented).

33. Carpel connation (0=syncarpous, 1=apocarpous all or most of length). Carpels are united only at their base in Acsmithia and Pancheria.

34. Style connation (0=free, 1=fused).

35. Appendage/ovary insertion (0=hypogyny, 1=epigyny).

36. Carpel number (0=three or more, 1=two).

37. Ovules per carpel (0=more than two, 1=two, 2=one). Data from H&D (1992).

38. Stylar canal (0=present, 1=absent). Data from H&D (1992).

39. Fruit morphology (0=ventrally dehiscent-septicidal, 1=indehiscent-appendaged, 2=indehiscent-drupaceous, 3=dorsally dehiscent-loculicidal).

40. Fruit dehiscence (0=basipetal, 1=circumbasal-acropetal). Cunonia species have a unique fruits, where the capsule opens at the level of the receptacle, the styles usually remain adherent to each other, and the direction of septa dehiscence is often acropetal.

41. Capsule column (0=adnate pair, 1=free pair, 2=single). Most Cunoniaceae fruits are composed of carpels that dehisce along their sutures, exposing two locules containing seeds. The seeds are borne in two rows in each locule, along axile placentae (pendulous in some indehiscent fruits). The degree of fusion of the central vascular tissue within developing fruits varies, being completely fused into a single column, or fused into a pair of bundles, with each bundle joining the inner edge of adjacent carpels (Dickison 1975c; 1984). This anatomical

variation appears related to visibly different morphologies in mature fruits.

Weinmannia, Pancheria, Cunonia, and Vesselowskya have a "single" central column. In many species this central column is prominent because it remains intact and upright between the separate carpels after fruit dehiscence. The column is less conspicuous in some species because it remains partially attached to one edge of a carpel, but it is visible after fruit dehiscence as a single, short stub near the receptacle. Other genera have pairs of columns in one of two forms. In one form (called "adnate pair"), the columns adhere to a carpel edge during dehiscence, and only by examining the fruit near the receptacle can the pair of columns be seen. In the other form (called "free pair"), each column detaches from the carpel edges in fruit, then the column divides near its apex with each bifurcation adjoining the styles of opposing carpels. These three patterns of column morphology are well described and illustrated by Godley (1983).

42. Seed wings (0=present, 1=absent). See Dickison (1984) for detailed images of seed-surface characters. Not scored for indehiscent fruits.

43. Seed hairs (0=absent, 1=present). Not scored for indehiscent fruits.

44. Seed papillae (0=absent, 1=present).

WOOD ANATOMY (Dadswell and Eckersley 1938; Ingle and Dadswell 1956; Carlquist 1977; Dickison 1977; 1980; Carlquist 1981).

45. Vessel plate perforations (0=mostly scalariform, 1=mostly simple). For scalariform plates the number of bars is considered too variable to be treated as alternative character states.

46. Ray structure (0=markedly heterogeneous, 1=fairly homogeneous). Parenchymatous ray cells are either of one (homogeneous) or two (heterogeneous) distinct sizes.

47. Vessel distribution (0=solitary, 1=solitary-multiples, 2=radial-multiples). Vessels are predominantly solitary, arranged in roughly equal proportions solitary to radial multiples, or are almost exclusively in radial multiples of 3-8.

48. Intervessel pitting (0=scalariform to opposite, 1=opposite, 2=transitional-opposite-alternate).

APPENDIX 3. Taxon by character matrix. See Appendix 2 for a description of characters and a key to state symbols. A question mark denotes missing data, whereas a dash indicates an inapplicable character. Each section of Weinmannia is scored: LEI=Leiospermum, WEI=Weinmannia, FAC=Fasciculata, SPI=Spicata, INS=Inspersa. See Appendix 1 for the delimits of Geissois and Cunonia EUs. EUs ordered as in Fig. 4.

OTUs/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Weinmannia.LEI	1	0/2	1	1	0	0	0	0	0	0	0	2/3	0	0	1	-	0	0	4	1	0	0
Weinmannia.WEI	1	0/2	1	1	0	0	0	0	0	0	0	1/2/3	0	0	1	-	1	0	4	1	0	0
Weinmannia.FAC	1	0/2	1	1	0	0	0	0	0	0	0	1/2/3	0	0	1	-	1	0	4	1	0	0
Weinmannia.SPI	1	0/2	1	1	0	0	0	0	0	0	0	1/2/3	0	0	1	-	0	0	4	1	0	0
Weinmannia.INS	1/2	0/2	1	1	0	0	0	0	0	0	0	1/2/3	0	0	1	-	0	0	4	1	0	0
Cunonia 1	1	0/2	1	1	0	0	0	0	0	0	0	2	0	0	1	-	0	0	4	1	0	0
Cunonia 2	1	0	1	0	0	0	0	0	0	0	0	2	0	0	1	-	0	0	4	1	0	0
Pancheria	2	0/2	1	1	0	0	0	0	0	0	0	2	0	0	1	-	0	0	2	1	0	0
Vesselowskya	1	1	1	0	0	0	1	0	0	0	0	1	0	0	1	-	1	0	4	0	0	0
Callicoma	1	2	1	0	0	0	0	0	0	1	1	0	-	0	1	-	1	0	2	0/1	1	-
Codia	1	2	0	-	0	0	0	0	0	0/1	0/1	0/2	-	0	1	-	0	0	2	0/1	0/1	0
Pullea	1/2	2	0/1	0	0	0	0	0	0	0	0	0	-	0	1	-	1	0	0/2	1	1	-
Ackama	1	0	1	0	1	0	1	0	0	0	0	3	0/1	0	1	-	1	0	0	0	0	0
Spiraeopsis	1	0	1	1	1	1	1	0	0	0	0	3	1	0	1	-	1	0	0	0	0	0
Opocunonia	1	0	1	1	0	0	1	1	0	0	0	3	0	0	1	-	0	0	1	0	0	0
Caldcluvia	1	2	1	1	0	0	1	0	0	0	0	3	-	0	0	0	0	0	1	0	0	0
Geissois 1	1	1	0/1	0	0	0	0/1	0	0	0	0	3	1	0	2	1	0	0	4	0	1	-
Geissois 2	1	1	1	0	0	0	0	0	0	0	0	3	1	0	0	1	0	0	4	0	1	-
Pseudoweinmannia	1	1	1	0	0	0	0	0	0	0	0	3	1	0	0	1	0	0	4	0	1	-
Lamanonia	1	1	1	0	0	0	0/1	0	0	0	0	3	1	0	0	0	0	0	4	0	1	-
Acrophyllum	2	2	1	0	0	0	0	0	0	0	0	0	-	0	1	-	0	0	1	0	0	0
Gillbeea	1	0	0/1	0	0	1	0	0	0	0	0	3	0	0	0	0/1	0	1	0	0	0	1
Aistopetalum	1	0	0/1	0	0	0	0	0	0	0	0	3	0	0	1	-	0	1	0	0	1	-
Eucryphia	1	0/2	0/1	0	0	0	0	0	0	0	0	3	0	0	1	-	0	-	3	1	0	0
Bauera	1	2	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	-	3	1	0	0
Anodopetalum	1	2	1	1	0	0	0	0	0	0	0	3	-	0	1	-	0	1	1	0	0	1
Platylophus	1	1	1	1	0	0	0	0	0	0	0	3	0	0	1	-	0	1	1	0	0	1
Ceratopetalum	1	1/2	1	1	0	0	0	0	0	0	0	3	0	0	1	-	0	1	1	0	0/1	1
Schizomeria	1	2	1	1	0	0	0	0	0	0	0	3	-	0	1	-	0	1	1	0	0	1
Davidsonia	0	0	1	0	0	0	0	0	0	0	0	3	1	0	-	-	0	1	0	0	1	-
Acsmithia	2	2	0/1	1	0	0	0	1	1	0	0	3	-	0	1	-	0	0	0	0	1	-
Spiraeanthemum	1	2	1	1	0	0	0	1	1	0	0	3	-	0	1	-	1	0	0	0	1	-
Brunellia	1/2	0/2	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0/1	0	1	-
Cephalotus	0	2	0	-	0	0	0	0	0	0	0	0	-	1	-	-	0	1	0	0	1	-
Aristotelia	0/1	2	1	0	0	0	0/1	0	0	0	0	0	-	1	-	-	0	1	1	0	0	1
Sloanea	0	2	1	1	0	0	0/1	0	0	0	0	0/1/3	-	0/1	-	-	0	0/1	0/1/3/4	0	0/1	1
Crinodendron	0/1	2	1	0	0	0	1	0	0	0	0	0	-	0	0	0	0	-	3	0	0	1
Elaeocarpus	0/1	2	0/1	1	0	0	0	0/1	0	0	0	0/1/3	-	0/1	0	0	0	0	4	0	0	1
Tetratheca	0/1/2	2	1	?	0	0	0	0	0	0	0	?	-	1	-	-	0	-	3	0	0	0

Appendix 3. Taxon by character matrix. See Appendix 2 for a description of characters and a key to state symbols. A question mark denotes missing data, whereas a dash indicates an inapplicable character. Each section of *Weinmannia* is scored: LEI=*Leiospermum*, WEI=*Weinmannia*, FAC=*Fasciculata*, SPI=*Spicata*, INS=*Inspersa*. See Appendix 1 for the delimits of *Geissois* and *Cunonia* OTUs.

24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0
0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0
0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0
0	0	0	0	1	0	0	1	0/1	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0
0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0
0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0
0	0	0	0	1	0	0/1	1	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0
0	0	0	0	1	0	0	1	0/1	1	-	0	1	1	0	0	0	-	0	0	0	0	0	0	0
0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	-	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0
0	0	0	0	1	0	0	0	-	0	0	1	1	0/1	0	1	-	-	-	-	0	1	0	0	0
0	0	0	0	1	1	0	1	1	0	0	0/1	1	0/1	0	1	-	-	-	-	0	0	0	0	0
0	0	0	0	1	0	0	1	1	0	0	0	0/1	0	0	0	0	0/1	1	1	0	0	0	1	0
0	0	0	0	1	0	0	1	1	0	0	0	0/1	0	1	0	0	1	0	0	1	1	0	1	2
0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	2	2
1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	2	2
1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	-	-	-	-	0	1	0	2	2
1	0/2	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	2	2
0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0
0	0	0	0	0	2	1	1	0	0	0	0	0	0/1	1	1	-	-	-	-	1	0	0	1	0
0	0	0	0	0	0	0	1	0	0	0	0	0	2	1	2	-	-	-	-	0	1	0	1	2
1	2	0	0	0	1	0/1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0/1	1	0
1	2	0	0/1	0	1	0	0	-	0	0	1	1	0	0	0	0	2	1	0	0/1	1	0	0	1
0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	-	-	-	0	0	1	1	1	0
0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	1	-	-	-	-	0	1	1	1	0
0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	-	-	-	-	0	1	1	1	0
0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	2	-	-	-	-	0	1	1	1	2
0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	2	-	-	-	-	0	1	1	1	0
0	0	0	0	0	0	0	1	1	1	-	0	0	1/2	0/1	0	0	-	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	1	1	-	0	0	1	0/1	0	0	-	0	0	0	0	0	0	0
0	0	0	0	1	0	?	1	0	1	-	0	0	1	1	0	0	-	1	0	0	1	0	1	0
0	0	0	0	1	0	0	0	-	1	-	0	0	1/2	0	0	0	-	?	0	?	1	1	0	2
2	1	1	1	1	0	?	0	-	0	1	0	1	1	-	2	-	-	-	-	?	1	0	2	2
1	2	1	0/1	1	0	?	0	-	0	1	0	0/1	0	-	3	0	-	1	0	0	1	0	0	1
1	0	1	1	1	0	?	0	-	0	1	0	0	0	-	3	0	-	1	0	?	1	0	2	2
1	0/2	1	1	1	0	?	0	-	0	1	0	0/1	0/1	-	2	-	-	-	-	?	1	0	?	1
0	1	1	1	1	0	?	0	-	0	1	0	1	0/1/2	-	3	0	-	1	1	0	1	?	?	?

APPENDIX 4. Vouchers for exemplars used in DNA sequencing, and the GenBank number of each sequence are given below. Collection information is only given for sequences not previously reported. Three species-level taxa are recognized for Davidsonia although only one is thus far described (G. Harden, pers comm.). {**Note: will database sequences when ms accepted**}

Genus	Species	Collection	Origin	TrnL-TrnF	rbcL
Cunoniaceae					
Ackama	paniculosa	Bradford 843	Australia	x	
Ackama	rosifolia	Bradford 909	New Zealand	x	
Acrophyllum	australe	Bradford 868	Australia	x	x
Acsmithia	elliptica	Bradford 613	New Caledonia	x	x
Anodopetalum	biglandulosum	Bradford 890	Australia	x	x
Bauera	rubioides	Bradford 730	Australia (U.S.)	x	
Bauera	rubioides L11174		Australia (U.S.)		
Bauera	sessiliflora	Bradford 729	Australia (U.S.)	x	
Caldcluvia	paniculata	Barnes s.n.	Chile (Australia)	x	x
Callicoma	serratifolia	Bradford 857	Australia	x	x
Ceratopetalum	gummiferum	Bradford 873	Australia	x	
Ceratopetalum	gummiferum L01895		Australia		
Codia	discolor	Bradford 600	New Caledonia	x	x
Cunonia	atrorubens	Bradford 614	New Caledonia	x	x
Cunonia	balansae	Bradford 617	New Caledonia	x	
Cunonia	capensis	Bradford 735	South Africa (U.S.)		x
Cunonia	macrophylla	Bradford 607	New Caledonia	x	
Davidsonia	'jerseyana'	Bradford 887	Australia	x	
Davidsonia	'johnsonii'	Bradford 851	Australia	x	
Davidsonia	pruriens	Hufford 1687	Australia (U.S.)		x
Eucryphia	cordifolia	Bradford 937	Chile (U.S.)	x	x
Eucryphia	moorei	Bradford 860	Australia	x	
Eucryphia	lucida L01918		Australia		
Geissois	benthamii	Bradford 859	Australia	x	x
Geissois	superba	Fortune Hopkins 5019	Fiji	x	
Gillbeea	adenopetala	Barnes s.n.	Australia	x	x
Pancheria	engleriana	Bradford 602	New Caledonia	x	
Pancheria	hirsuta	Bradford 610	New Caledonia	x	
Platylophus	trifoliatus	Goldblatt 10888	South Africa	x	x
Pseudoweinmannia	lachnocarpa	Bradford 858	Australia	x	x
Pullea	cf. glabra	Bradford 585	Fiji	x	x
Schizomeria	ovata	Bradford 850	Australia	x	
Spiraeanthemum	samoense	Bradford 809	Samoa	x	
Spiraeopsis	celebica	Bradford 840	Solomon Islands	x	x
Vesselowskya	rubifolia	Bradford 879	Australia	x	x
Weinmannia	dichotoma	Fortune Hopkins 5053	New Caledonia	x	
Weinmannia	raiatensis	Bradford 927	Society Islands	x	x
Weinmannia	samoensis	Bradford 800	Samoa	x	
Weinmannia	sylvicola	Bradford 912	New Zealand	x	

Weinmannia	clemensiae	Fortune Hopkins 5011	Malaysia	x	
Weinmannia	fraxinea	Bradford 578	Malaysia	x	
Weinmannia	exigua	Bradford 814	Solomons	x	
Weinmannia	minutiflora	Malcomber 2874	Madagascar	x	
Weinmannia	sanguisugarum	Bradford 715	Madagascar	x	
Weinmannia	madagascariensis	Bradford 653b	Madagascar	x	x
Weinmannia	rutenbergii	Malcomber 2880	Madagascar	x	
Weinmannia	bangii	Bradford 525	Bolivia	x	x
Weinmannia	tinctoria	D'Argent, MAU 22790	Mauritius	x	
Brunelliaceae					
Brunellia	colombiana	Bradford 753	Colombia	x	x
Brunellia	oliveri	Skinner 43	Bolivia	x	x
Cephalotaceae					
Cephalotus	follicularis	T.D.Macfarlane 2549	Australia	x	
Cephalotus	follicularis L01894		Australia		
Connaraceae					
Connarus	conchocarpus U06798				
Elaeocarpaceae					
Aristotelia	chiliensis	Bradford 934	Chile (U.S.)	x	x
Aristotelia	peduncularis	Bradford 895	Australia	x	
Aceratium	ferrugineum L28947				
Crinodendron	patagua	Bradford 935	Chile (U.S.)	x	x
Elaeocarpus	reticulatus	Bradford 847	Australia	x	x
Sloanea	australis	Bradford 862	Australia	x	
Oxalidaceae					
Oxalis	dillenii L01938				
Tremandraceae					
Tetratheca	rupicula	Bradford 871	Australia	x	
Platytheca	verticellata L01944				

APPENDIX 5. Description of tribes in Cunoniaceae. Synapomorphies of each tribe are in italics.

Cunonieae (R. Br.) Schrank & Mart., Hort. Reg. Monac.: 125 (1829).
Cunonia L., Syst. Nat., ed. 10, 2: 1013, 1025, 1368 (1759).
Including Weinmannia, Pancheria, and Vesselowskya.

Trees and shrubs. Stipules interpetiolar. Leaves decussate or whorled, imparipinnate or unifoliolate, stipels absent. Inflorescence racemose or a spherical head (Pancheria); flowers maturing synchronously to acropetally. Flowers bisexual or unisexual and often dioecious; petals present; diplostemonous; pollen tricolporate; ovary bicarpellate, syncarpous or partially apocarpous (Pancheria). Fruits capsular, with a single vertical column bearing seeds; seeds appendaged by wings or trichomes (Weinmannia).

Codieae G.Don, Gen. Hist. 3: 197, 202 (1834).
Codia J.R.Forst. & G.Forst., Char. gen. pl. 59, t30 (1776).
Including Pullea and Callicoma.

Trees and shrubs. Stipules medial. Leaves decussate or rarely whorled, unifoliolate, subsidiary cells anomocytic or anisocytic (some Codia). Inflorescence capitate or paniculate (Pullea glabra); flowers maturing synchronously. Flowers bisexual; petals absent or present (some Codia); mostly diplostemonous; pollen dicolporate or tricolporate (Codia); ovary bicarpellate, syncarpous, superior or half inferior. Fruits indehiscent or capsular; seeds lacking appendages.

Caldcluvieae J.C. Bradford & R.W. Barnes, trib. nov.

TYPUS: Caldcluvia D. Don, Edinburgh New Philos. J. 9: 92. 1830.
Including Ackama, Spiraeopsis, and Opocunonia.

Arbores. Folia decussata, imparipinnata unifoliolatave; stipulis medianis lateralibusve; stipellis praesentibus absentibusve; foliolis trichomatibus simplicibus orbiculari-glandularibus (Ackama et Spiraeopsis) stellatisve (Spiraeaopsis) vestitis, secus costam nervorum secundariorum in axillis trichomatum caespitibus praeditis.

Inflorescentia paniculata cymiformisve, florum maturatione simultanea. Flores bisexuales, diplostemoni, saltem in Opocunonia Spiraeopsi Ackamaque protrandri; petalis praesentibus; polline tricolporato dicolporatove (Caldcluvia); gynoecio ex carpellis 2 ad 6 constante, plerumque syncarpo, stylis liberis. Fructus capsularis; seminibus alatis, vel exalatis comosisque.

Trees. Stipules medial or lateral. Leaves decussate, imparipinnate or unifoliolate, stipels present or absent; trichomes simple, orbicular-glandular (Ackama and Spiraeopsis) or stellate (Spiraeopsis); tuft domatia along midvein. Inflorescence paniculate to cymiform; flowers maturing synchronously. Flowers bisexual, protandrous (Opocunonia, Spiraeopsis and Ackama?) or not; pollen tricolporate or dicolporate (Caldcluvia); petals present; diplostemonous; ovary with 2-6 carpels, mostly syncarpous, styles free. Fruits capsular; seeds winged, or not winged and with hairs.

Geissoieae Endl. ex Meisn., Pl. Vasc. Gen.: Tab. Diagn. 138, Comm. 101 (1838).
Geissois Labill., Sert. austro-caledon. 50, t50 (1825).
Including Pseudoweinmannia and Lamanonia.

Trees and shrubs. Stipules lateral or axillary. Leaves decussate, palmately compound, stipels present. Inflorescence racemose; flowers maturing synchronously to acropetally. Flowers bisexual; petals absent; androecium polystemonous; pollen dicolporate; ovary bicarpellate. Fruit capsular or indehiscent; seeds winged or not.

Schizomerieae J.C. Bradford & R.W. Barnes, trib. nov.

TYPUS: Schizomeria D. Don, Edinburgh New Philos. J. 9: 94. 1830.
Including Anodopetalum, Ceratopetalum and Platylophus.

Arbores fruticesve. Folia decussata, trifoliolata unifoliolatave; stipulis medianis; stipellis absentibus. Inflorescentia cymiformis thyrsoideave florum maturatione centrifuga, vel ex flore solitario constans (Anodopetalum). Flores bisexuales staminative, diplostemoni;petalis apice incisis vel (pro maxima parte in Ceratopetalo)

absentibus; gynoecio ex carpellis 2 vel (interdum in Schizomeria) 3 constante. Fructus drupaceus (Schizomeria) nuculiformis (Ceratopetalum) vesiculatus (Platylophus) capsularisve (Anodopetalum); seminibus exalatis.

Trees and shrubs. Stipules medial. Leaves decussate, trifoliolate or unifoliolate, stipels absent. Inflorescence cymiform to thyrsoid or solitary (Anodopetalum); flowers maturing centrifugally. Flowers bisexual or male; petals with incised apex, or absent (most Ceratopetalum); diplostemonous; bicarpellate or tricarpellate (some Schizomeria). Fruit drupaceous (Schizomeria), nut-like (Ceratopetalum), bladder-like (Platylophus) or capsular (Anodopetalum); seeds unwinged.

Spiraeanthemeae Engl., Engl. & Prantl., Nat. Pflanzenfam. ed. 2, 18a: 237 (1928).
Spiraeanthemum A.Gray, Proc. Amer. Acad. Arts Sci. 3: 128 (1854). Including Acsmithia.

Trees and shrubs. Stipules medial. Leaves decussate or whorled, unifoliolate; epidermal glands present; pocket domatia along midvein. Inflorescence paniculate; flowers maturing synchronously. Flowers bisexual, or unisexual and dioecious; petals absent; diplostemonous; ovary of 2-6 free carpels. Fruit follicular; seeds winged.

FIG. 1. Bootstrap consensus tree and bootstrap values for rbcL gene. Arrow indicates a node that was unresolved in the strict consensus of shortest trees. Bold taxa are traditionally placed in Cunoniaceae, a box surrounds Elaeocarpaceae genera (including Platytheca in the Tremandraceae), and all other genera are traditionally in separate families. "Cunon sp." represents a poorly known shrub from New Zealand (called 'X-it' by Garnock-Jones et al. 1996). The clade comprising Caldcluvia s.l. is labeled.

FIG. 2. Strict consensus and bootstrap cladogram of the trnL-trnF region. Gray lines show the clades found when all indels were excluded. Numbers above branches are bootstrap values (value with indels/value

excluding all indels), dashes indicate a bootstrap support less than 50%, 0 indicates a clade not present in the strict consensus tree for one of the two analyses. Below one branch is a bootstrap value in parentheses for analysis 3, which was the only branch differing by more than 5% from analysis 1. Where they are informative, insertions and deletions >2 bp are labeled: D=deletion in intron, I=insertion in intron, d=deletion in spacer, i=insertion in spacer. The section of each Weinmannia clade is labeled to its right. Taxa from Madagascar, the Comores, the Mascarenes or South Africa are in gray boxes, taxa from the Americas are in outlined boxes. All other taxa are from Malesia, Australia or the South Pacific. The informal names used to discuss four clades and Caldcluvia s.l. are labeled.

FIG. 3. Phylogram from combined chloroplast DNA sequence data, one of twelve most parsimonious trees. Bootstrap values are above branches, decay values below branches. Taxa in bold are part of a recircumscribed Cunoniaceae.

FIG. 4. Strict consensus tree (solid lines) from a parsimony analysis of morphological characters using a constraint tree (bold branches) based on clades found in molecular analyses. DNA was unavailable for taxa in bold. Small arrows indicate nodes not seen in the strict consensus of molecular analyses. M shows branches found in the strict consensus of an unconstrained analysis of morphology that are compatible with the constraint tree, with the clade of Weinmannia sections not resolved in the constrained analysis. Tribes are in gray boxes, with a list of morphological synapomorphies indicated for each tribe. The form of flower-bearing axes is represented for each genus or clade. Pullea is polymorphic, and Anodopetalum has solitary flowers or rarely 3-flowered cymes.

FIG. 5. Hypotheses of morphological evolution among tribes and genera in Cunoniaceae. Bold taxa are tribes, unplaced genera are in italics. Solid dashes denote the origin of a character state, open dashes are reversals to plesiomorphic states relative to Cunoniaceae and

sister groups (reversals within tribes are not shown). Fruit characters are illustrated to the right of each EU. The number of carpels may vary within each fruit type illustrated.

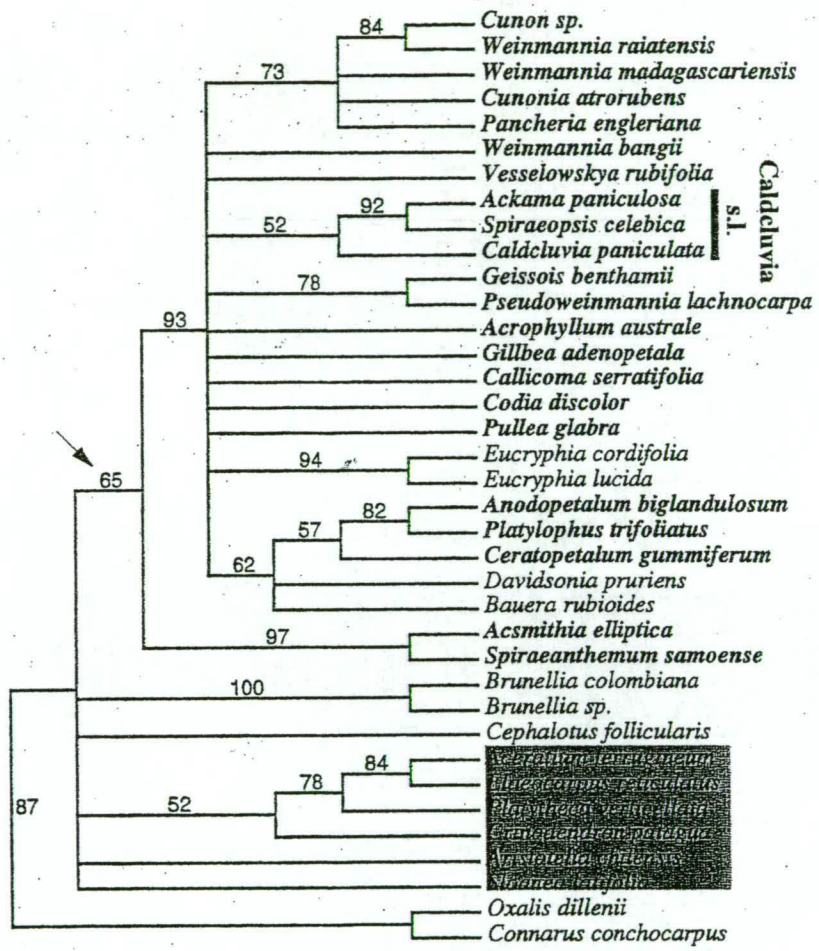

Fig. 1. Bootstrap consensus tree for *rbcL* gene. Arrow indicates a node that was unresolved in the strict consensus of shortest trees. Bold taxa are traditionally placed in the Cunoniaceae, a box surrounds Elaeocarpaceae genera (including *Platytheca* in the Tremandraceae), and all other genera are in separate families. "Cunon sp." represents a poorly known shrub from New Zealand. The clade comprising *Caldcluvia* s.l. is labeled.

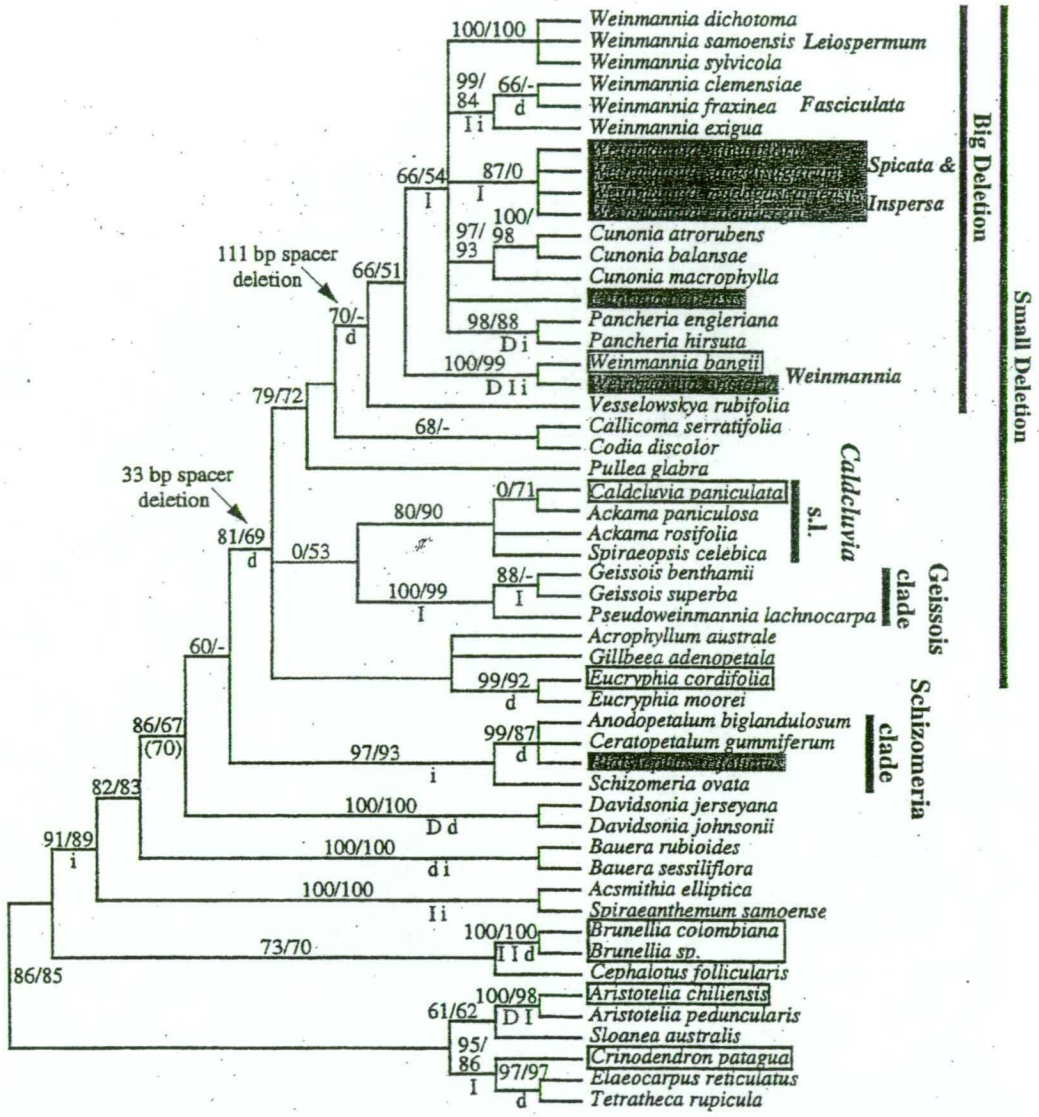

Fig. 2. Strict consensus and bootstrap cladogram of the *trnL-trnF* region. Grey lines show the clades found when all indels were excluded. Numbers above branches are bootstrap values (value with indels/value excluding all indels), dashes indicate a bootstrap support less than 50%, 0 indicates a clade not present in the strict consensus tree for one of the two analyses. Below one branch is a bootstrap values in parentheses for analysis 3, which was the only branch differing by more than 5% from analysis 1. Where they are informative, insertions and deletions >2 bp are labeled: D=deletion in intron, I=insertion in intron, d=deletion in spacer, i=insertion in spacer. The section of each *Weinmannia* clade is labeled to its right. Taxa from Madagascar, the Comores, the Mascarenes or South Africa are in grey boxes, taxa from the Americas are in outlined boxes. All other taxa are from Malesia, Australia or the South Pacific. The informal names used to discuss four clades and *Caldcluvia* s.l. are labeled.

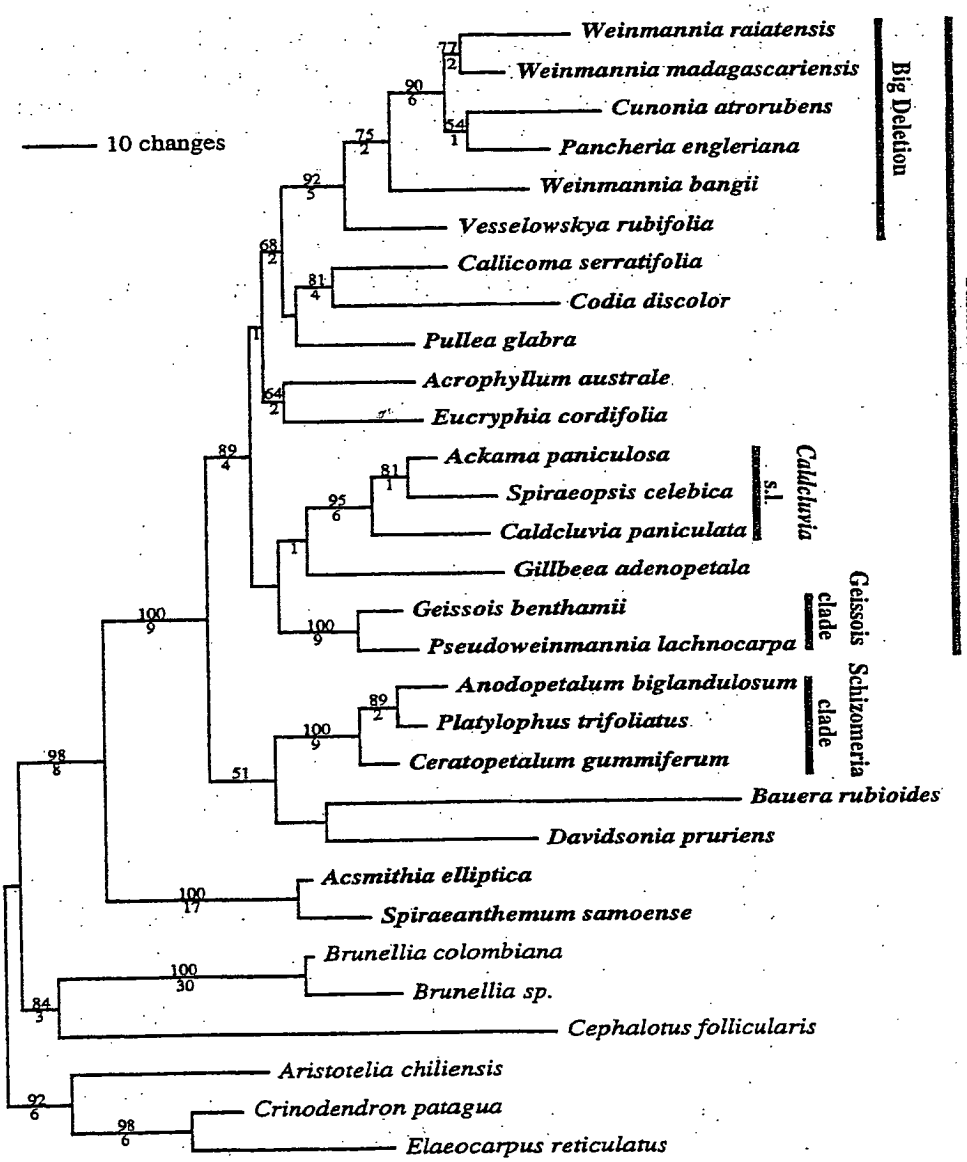

Fig. 3. Phylogram from chloroplast DNA sequence data, one of twelve most parsimonious trees. Bootstrap values are above branches, decay values below branches. Taxa in bold are part of a recircumscribed Cunoniaceae.

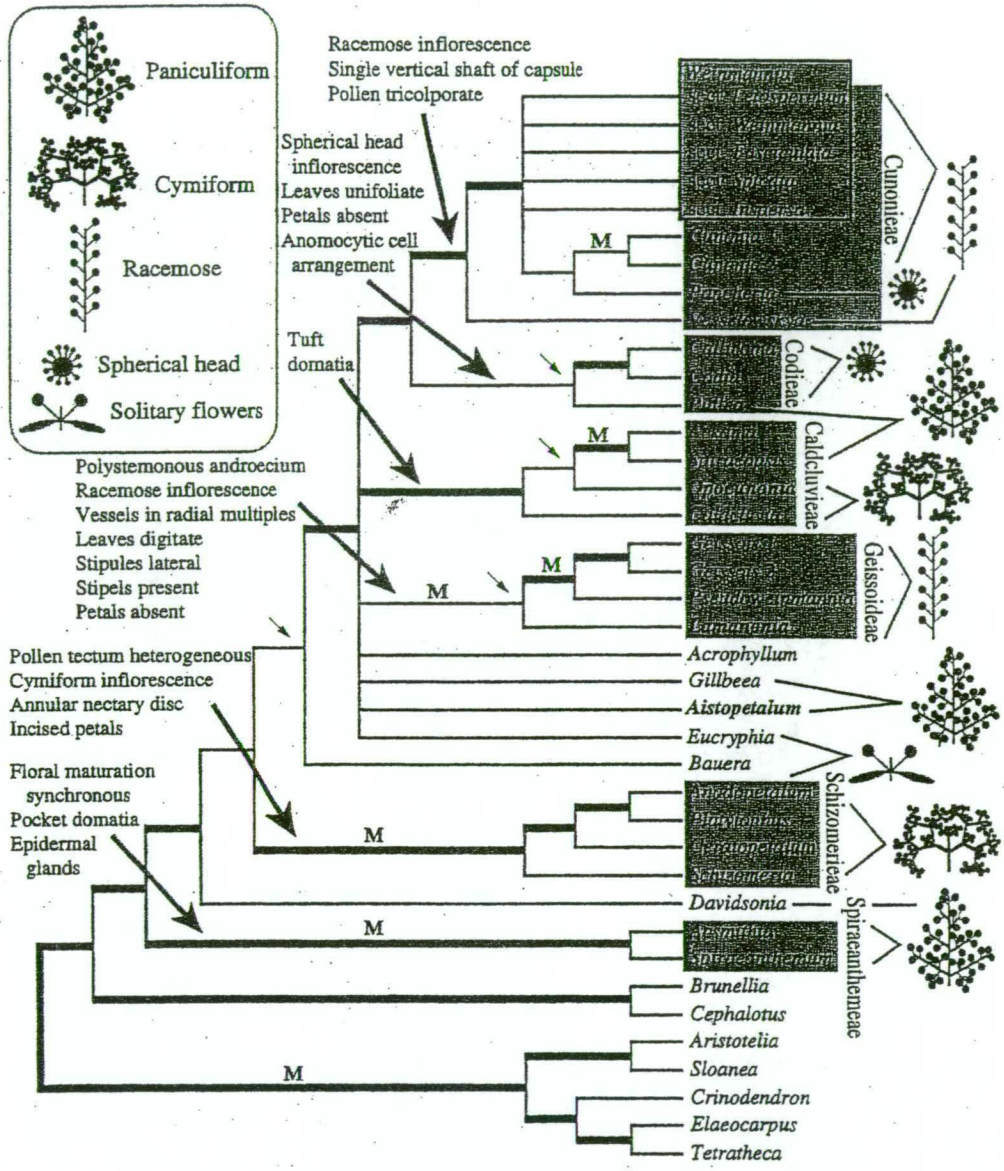

Fig. 4. Strict consensus tree from a parsimony analysis of morphological characters using a constraint tree (bold branches) based on clades found in molecular analyses. DNA was unavailable for taxa in bold. Small arrows indicate nodes not seen in molecular analyses. M shows branches found in the strict consensus of an unconstrained analysis of morphology. Tribes are in grey boxes, with a list of morphological synapomorphies indicated for each tribe. The form of flower-bearing axes is represented for each genus or clade, except for *Acrophyllum* which has a unique form. *Pullea* is polymorphic, and *Anodopetalum* has solitary flowers or rarely 3-flowered cymes.

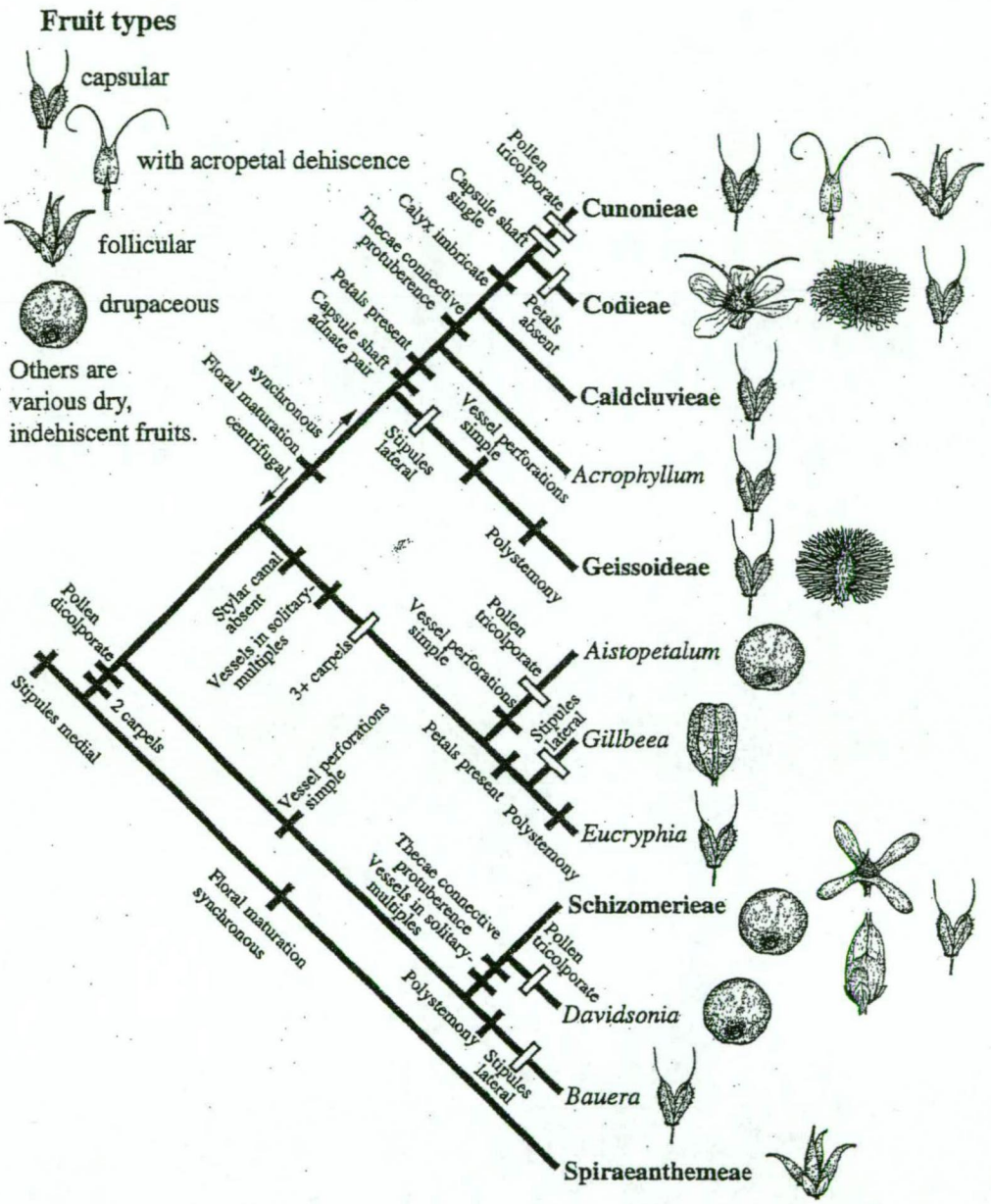

Fig. 5. Hypotheses of morphological evolution among tribes and genera in the Cunoniaceae. Bold taxa are tribes, unplaced genera are in italics. Solid dashes denote the origin of a character state, open dashes are reversals to plesiomorphic states relative to the Cunoniaceae and sister groups. Fruit characters are illustrated to the right of each OTU. The number of carpels may vary within each fruit type illustrated.

Appendix 2. Taxonomic authorities for the extant and fossil species and genera used in this study.

Extant Taxa

Ackama	A. Cunn.
A. australiensis	(Schlechter) C.T. White
A. paniculosa	Beuzeville & C.T. White
A. rosaefolia	A. Cunn.
Acrophyllum	Benth.
A. australe	(Cunn.) Hoogl.
Acsmithia	Hoogland
A. austro-caledonica	(Brongn. & Gris) Hoogl.
A. davidsonii	(F.Muell.) Hoogl.
A. densiflora	(Brongn. & Gris) Hoogl.
A. integrifolia	(Pulle) Hoogl.
A. meridonalis	Hoogl.
A. parvifolia	(Schlechter) Hoogl.
A. pulleana	(Schlechter) Hoogl.
A. reticulata	(Schlechter) Hoogl.
Aistopetalum	Schlechter
A. multiflorum	Schlechter
A. viticoides	Schlechter
Anodopetalum	A.Cunn. ex Endl.
A. biglandulosum	(A.Cunn. ex Hook.) Hook. f.
Bauera	Banks ex. Andrews
B. capitata	DC.
B. microphylla	DC.
B. rubioides	Andrews
B. sessiliflora	F.Muell.
Caldcluvia	D. Don.
C. paniculata	(Cav.) D. Don
Callicoma	Andrews
Callicoma serratifolia	Andrews
Ceratopetalum	Sm.
C. apetalum	D. Don
C. corymbosum	C.T. White
C. gummiferum	Sm.
C. macrophyllum	Hoogl.

C. succirubrum	C.T. White
C. virchowii	F.Muell.
Codia	J.R.Forst. & G.Forst.
C. albifrons	Viell. ex Guillam.
C. discolor	(Brongn. and Gris.) ex. Guillaum.
C. montana	Forst.
C. nitida	Schlecht.
C. obcordata	Brongn. & Gris
Cunonia alticola	Guill.
C. atrotrubens	Schltr.
C. aoupiniensis	Hoogland
C. austro-caledonia	Brongn. & Gris ex Guillaumin
C. balansae	Brongn. & Gris
C. capensis	L.
C. lenormandii	Vieill. ex Brongn. & Gris
C. linearisepala	(Guillaumin) Bernardi
C. macrophylla	Brongn. & Gris
C. montana	Schltr.
C. pterophylla	Schlechter
C. pulchella	Brongn. & Gris
C. purpurea	Brongn. & Gris
Davidsonia	F. Muell.
D. jerseyana	F.M. Bailey
D. johnsonii	J.Williams & G.Harden
D. pruriens	F. Muell.
Eucryphia	Cav.
E. cordifolia	Cav.
E. glutinosa	(Poepp. et Endl.) Baill.
E. jinksii	P.I.Forst
E. lucida	(Labill.) Baill.
E. milliganii ssp. *milliganii*	Hook.f.
E. milliganii ssp. *pubescens*	R.W.Barnes, G.J.Jord., R.S.Hill & C.J.McCoull
E. moorei	F.Muell.
E. wilkiei	B.Hyland
Geissois	Labill.
G. benthamii	F.Muell.
G. biagiana	F.Muell. (F.Muell.)
G. hirsuta	Brogn. & Gris

G. montana	Vieill.
G. polyphylla	Lecard
G. pruinosa	Brogn. & Gris
G. racemosa	Labill.
Gillbeea	F.Muell.
G. adenopetala	F.Muell.
G. papuana	Schltr.
Lamanonia	Vell.
L. speciosa	Camb.
Opocunonia	Schlechter
O. nymanii	(K. Schum.) Schlechter
Pancheria	Brogn. & Gris
P. alaternoides	Brogn. & Gris
P. elegans	Brogn. & Gris
P. hirsuta	Vieill.
Platylophus	D. Don
P. trifoliatus	D. Don.
Pseudoweinmannia	Engl.
P. lachnocarpa	(F. Muell.) Engl.
Pullea	Schlechter
P. glabra	Schlechter
P. mollis	Schlechter
P. stutzeri	(F.Muell.) Gibbs
Schizomeria	D.Don
S. iliciana	(Ridl.) Schltr.
S. katastega	Mattf.
S. ovata	D.Don
S. parvifolia	Perry
S. serrata	(Hook)
S. whitei	Mattf.
Spiraeopsis	Miq.
S. brassii	Perry
S. celebica	Blume
S. clemensiae	Perry
S. fulva	(Schlechter) Perry
S. papuana	(Pulle) Perry
S. rufa	(Schlechter) Perry
Spiraeanthemum	A. Gray
S. bougainvillense	Hoogl.

S. katakata	Seem.
S. macgillivrayi	Seem.
Vesselowskya	Pampanini
V. rubifolia	(F. Muell.) Pampan.
Weinmannia	L.
W. affinis	A. Gray
W. balbisiana	Kunth.
W. bansio	Rusby
W. bojeriana	Tul.
W. burseraefolia	Standl.
W. cochensis	Hieron.
W. clemensiae	Steenis
W. crassifolia	Ruiz & Pav.
W. decora	Tul.
W. ellattantha	Diels
W. eriocarpa	Tul.
W. fagaroides	Kunth
W. fraxinea	Sm. ex D. Don.
W. glabra	L.f.
W. humblottii	Baill.
W. intermedia	Schltr. & Cham.
W. microphylla	Ruiz & Pav.
W. minutifolia	Baker
W. parviflora	G. Forst.
W. paulliniifolia	Pohl ex Ser.
W. pentaphylla	Ruiz & Pav.
W. pinnata	L.
W. pubescens	Kunth
W. pullei	Schltr.
W. racemosa	L.f.
W. richii	A. Gray
W. rollotii	Killip
W. rutenbergii	Engl.
W. serrata	Brongn. & Gris
W. sorbifolia	Kunth
W. sylvicola	Sol. ex A. Cunn.
W. tomentosa	L.f.
W. trichophora	Pamp.
W. trichosperma	Cav.

W. urdanetensis	Elmer
W. wercklei	Standl.

Fossil Taxa

Acsmithia grandiflora	R.J. Carpenter & A.M. Buchanan
Banksieaephyllum attenuatum	Hill & Christophel
Banksieaephyllum taylori	R.J.Carp., G.J.Jord. & R.S.Hill
Caldcluvia mirabilis	Dusén
Caldcluvioxylon collinsense	Shanzhen & Qingzhi
C. propaniculata	Torres
Callicoma pannonica	Ung.
C. primaeva	Ett.
Ceratopetalum gilesii	Ett.
C. kaikoraiense	Oliver
C. maslinensis	R.W.Barnes & R.S.Hill
C. pacificum	Oliver
C. praearbutoides	Ett.
C. primigenium	Ett.
C. priscum	Holmes & Holmes
C. radobojanum	Ett.
C. rivulare	Ett.
C. westermannii	R.W.Barnes & R.S.Hill
C. wilkinsonii	(Ett.) Holmes & Holmes
C. woodii	Ett.
Codia australiensis	R.W.Barnes & R.S.Hill
Concolpites leptos	Partridge
Eucryphia aberensis	R.S.Hill
E. falcata	R.S.Hill
E. gregorii	Deane
E. microstoma	R.S.Hill
E. mucronata	R.W.Barnes & G.J.Jord.
E. reticulata	R.W.Barnes & G.J.Jord.
Euproteaciphyllum	R.J.Carp., G.J.Jord. and R.S.Hill
Lomatia mirabilis	(Dusén) Li
Phyllites yallournensis	Cookson & Duigan
Schizomeria tasmaniensis	R.J. Carpenter & A.M. Buchanan
Weinmanniaphyllum bernardii	R.J. Carpenter & A.M. Buchanan
Weinmannia brittoni	Engelhardt
Weinmannioxylon pluriradiatum	Petriella
W. multiperforatum	Petriella

Appendix 3. List of plant material examined in this study.

Those taxa with an asterix were examined from fresh and/or preserved material collected in the field or propagated *ex situ* from seed or cuttings.
Specimens originally housed at the Canberra Botanical Gardens (Australia) are denoted by the CBG prefix but are now housed in the Australian National Herbarium (CANB). Some specimens were not numbered or databased in the CANB collection.
The Barnes and Alastair Watt collections used in this study are housed in the School of Plant Science, University of Tasmania. Representative samples of each taxon from these collections will be lodged in the Tasmanian Herbarium (HO) with reference to this study.
The specimens identified by collector and collection number were donated by Jason C. Bradford (Washington University and Missouri Botanic Garden, MO) or Helen F. Hopkins (Kew) and will be lodged in HO. Specimens were also examined from the Atherton Herbarium (QRS) and University of Minnesota (MIN).

Specimens Examined

***Ackama** *australiensis*, Australia CANB035755; HO328832, HO118424, Barnes collection; **A. paniculosa*, Australia CANB038242, CBG034994, CBG8413907, MIN125337; **A. rosaefolia*, New Zealand CBG7606958, HO316338, HO79050, MIN125323.
***Acrophyllum** australe*, Australia CANB026583, CANB025532, CBG8411648, MIN125324.
***Acsmithia** austro-caledonica*, New Caledonia CANB not databased; **A. davidsonii*, Australia CBG9102735, HO330085, HO314529, Barnes collection; *A. densiflora*, New Caledonia HO131657, HO302120; *A. integrifolia*, Papua New Guinea CANB not databased; *A. meridonalis*, New Caledonia CBG00477863, CANB not databased; *A. parvifolia*, Papua New Guinea CANB not databased (2); *A. pulleana*, Irian Jaya 14233, CANB not databased; *A. reticulata*, Papua New Guinea CBG96278, CANB not databased.
***Aistopetalum** multiflorum*, Papua New Guinea, CANB197309, CANB197310, CANB243539, CANB230903, CANB not databased; *A. viticoides*, Papua New Guinea CANB47859, CANB386201, CANB99383, CANB389320.
***Anodopetalum** biglandulosum*, Tasmania HO406841, HO315589, HO126638, HO126691, HO403744, HO403998, HO144812, HO404707, HO404848,

HO405033, HO405320, HO405943, HO406070, HO406350, HO15877, HO83333, HO42584, HO35419, HO121967; Barnes collection (see Barnes and Rozefelds 2000, Appendix 1).

Bauera *capitata*, Australia CBG007815, CBG049511, CBG8311076; *B. microphylla*, Australia CANB040488, CANB030879; **Bauera rubioides*, Australia CBG014618, CBG019903, CBG 9306103, Tasmania HO406503, HO401651, HO315299, HO315864, HO316946, HO313733, HO126141, HO410441, HO409006, HO407351, HO400399, HO409165, HO303591, HO404124, HO404180, HO404474, HO404706, HO408931, HO411655, HO11955, HO126280, HO404413, HO404995, HO405491, HO405948, HO406199, HO407259, HO407270, HO412314, HO303849, HO400410, HO320149, Barnes collection; **B. sessiliflora*, Australia CBG012942, CBG061189, Barnes collection.

Caldcluvia *paniculata*, Chile Barnes collection.

Callicoma *serratifolia,* Australia CBG446776, HO13810, HO15899, HO10849, HO15901, HO302085, HO15903, HO15902, HO15905, Barnes collection.

Ceratopetalum *apetalum*, Australia CBG860082, CANB not databased, HO15911, HO123036, HO64367; **C. gummiferum*, Australia HO311543, HO15918, HO10861, HO15916; *C. corymbosum*, Australia CANB250843; **C. succirubrum*, Australia CANB00476003, Papua New Guinea CANB not databased, Papua New Guinea CBG170621; **C. virchowii*, Australia CANB not databased (2), Barnes collection; **C.* sp. nov. 1 'Mt Hemmant', Australia Barnes collection; **C.* sp. nov. 2 'Mt Lewis', Australia Barnes collection.

Codia *albifrons*, New Caledonia CANB232284; *C. discolor*, New Caledonia, Alastair Watt 96/007, CANB not databased; *C. montana*, New Caledonia CANB232286; *C. ?montana*, New Caledonia HO131517; *C. nitida*, New Caledonia CANB144745, HO131616, *Bradford and Hopkins 622* (HO); *C. obcordata*, New Caledonia CANB120331, CANB not databased; *C. spathulata*, New Caledonia CANB120323; *Codia* sp., New Caledonia, Alastair Watt 96/025, Alastair Watt 96/026; *Codia* sp. seedling, New Caledonia HO444879.

Cunonia *alticola*, New Caledonia *Bradford and Hopkins 611* (HO); *C. atrorubens*, New Caledonia CANB121306, not databased; *C. aoupiniensis*, New Caledonia HO12104; *C. austro-caledonica*, New Caledonia CANB203410; *C. balansae*, New Caledonia CANB284848; **C. capensis*, South Africa not databased; *C. lenormandii*, New Caledonia CANB284839; *C. linearisepala*, New Caledonia CANB283275; **C. macrophylla*, New Caledonia Alastair Watt 96/011, HO131619, Barnes collection; *C. montana*, New Caledonia *Bradford and Hopkins 609* (H); *C. pterophylla*, New Caledonia CANB284850, HO15907; *C. pulchella*, New Caledonia CANB137149; *C. purpurea*, New Caledonia CANB232756, not databased, Alastair Watt 96/039.

***Davidsonia** *pruriens*, Australia CANB475821, CANB475822, CANB338852, CANB199492, CANB475841, CANB not databased, CANB034201; *D.* sp. nov., Australia CBG8900665, CBG9003564.

***Eucryphia** *cordifolia*, Chile Barnes collection; **E. glutinosa*, Chile Barnes collection; **E. jinksii*, Australia Barnes collection; **E. lucida*, Tasmania; **E. milliganii* ssp. *milliganii* and E. milliganii ssp. pubescens, Tasmania Barnes collection (see Barnes *et al.* 2000); **E. moorei*, Australia Barnes collection; **E. wilkiei*, Australia Barnes collection.

***Geissois** *benthamii*, Australia CANB 8404064, 189660, MIN 125332; **G. biagiana*, Australia CANB 00477576, CANB246925, CANB246926, CANB477577, CBG9102509; *G. hirsuta*, New Caledonia 120324; *G. montana*, New Caledonia 144764; *G. polyphylla*, New Caledonia *Bradford 630* (HO); *G. pruinosa*, New Caledonia 144740, HO127581; *G. racemosa*, New Caledonia 120410; *G. velutina*, New Caledonia ANH 308229, 146087; *Geissois* sp., New Caledonia 284849; *Geissois* sp. 2, New Caledonia Alastair Watt 96/054; *Geissois* sp. 3, New Caledonia HO131484; *Geissois* sp. 4, New Caledonia HO131670.

***Gillbeea** *adenopetala*, Australia CANB89031, CANB89033, CANB261612, CANB372266, CANB372268, HO444729, Barnes collection; *G. papuana*, Papua New Guinea CANB203070.

***Lamanonia** *speciosa*, Paraguay CANB347444, CANB2174.

***Opocunonia** *nymanii*, Papua New Guinea CANB308221, CANB308228, CANB308243, QRS27414, QRS27413, QRS27416.

***Pancheria** *alaternoides*, New Caledonia CANB232273; *P. brunhesii*, New Caledonia *Bradford and Hopkins 616* (HO); *P. communis*, New Caledonia HO131659; *P. confusa*, New Caledonia CANB120389; *P. elegans*, New Caledonia CANB232274; *P. engleriana*, New Caledonia CANB232275; *P. hirsuta*, New Caledonia Alastair Watt 96/031; *P. gatopensis*, New Caledonia CANB232285; *P. multijuga*, New Caledonia CANB144779; *P. phylliraeoides*, New Caledonia *Bradford and Hopkins 620* (HO); *P. reticulata*, New Caledonia *Bradford and Hopkins 618* (HO); *Pancheria* sp., New Caledonia Alastair Watt 96/010; *Pancheria* sp., New Caledonia *Bradford and Hopkins 625* (HO).

***Platylophus** *trifoliatus*, South Africa Barnes collection.

***Pseudoweinmannia** *lachnocarpa*, Australia CBG8604170, CANB477832, CANB221592, MIN 125336.

***Pullea** *glabra*, Papua New Guinea CANB not databased; *P. glabra* var. *glabra* Papua New Guinea CBG8312845; *P. glabra* var. *verticillata*, Papua New Guinea CANB43236; *P. mollis*, Papua New Guinea CBG8300149; **P. stutzeri*, Australia CBG9102510, CANB not databased, HO118423.

Schizomeria *iliciana*, Irian Jaya CANB00477848; *S. katastega* Papua New Guinea, CANB308237; **S. ovata*, Australia CBG8804987, CANB310742, CANB9313893, MIN 125330, HO59812, Barnes collection, Papua New Guinea CBG8604209; *S. parvifolia*, Papua New Guinea CANB00477850; *S. serrata*, Papua New Guinea CANB308250, CANB386330, CBG 8313565; **S. whitei*, Australia CANB261880, CBG00476008, Barnes collection.

Spiraeanthemum *bouganvillense*, Papua New Guinea CANB141016, CANB141017; *S. katakata*, Fiji CANB33560; *S. macgillirayi*, Papua New Guinea CANB308218, New Britain CANB169892, New Hebrides CANB283268; *S.* sp., Fiji *Hopkins and Bradford 5020* (HO).

Spiraeopsis *brassii*, Papua New Guinea CBG8503458, CANB not databased, QRS83062, QRS27416; *S. celebica*, New Britain CANB308210, Papua New Guinea CANB178819, QRS82213; *S. clemensiae*, Papua New Guinea CANB43957, CANB not databased; *S. fulva*, Irian Jaya CANB00477854; *S. papuana*, Papua New Guinea CANB184736, CANB not databased (2), QRS27415; *S. rufa*, Papua New Guinea CANB83388, CANB134967, QRS27444, QRS27444.

Vesselowskya *rubifolia*, Australia CBG029049, CBG57699, CANB122634, CANB122635, CANB80335, MIN not databased.

Weinmannia *affinis,* Fiji *Hopkins and Bradford 5037* (HO), Fiji *Hopkins and Bradford 5021* (HO); *W. balbisiana*, Honduras *D'Arcy 17892* (HO); *W. bansio*, Peru *Núñez and Paycarmayta 13108* (HO); *W. blumei*, Papua New Guinea CBG 8312190, 00477856; *W. bojeriana*, Madagascar *Kotozafy 77* (HO), *van der Werff, Malcomber, Gray and Rapanarivo 12586* (HO); *W. brachystachya*, Ecuador *Palacios and Tipaz 10551* (HO); *W. burseraefolia*, Costa Rica *Bello 1338* (HO); *W. camiguinensis*, Philippines 386206; *W. cochensis*, Colombia 36958; *W. clemensiae*, Borneo 175285; *W. crassifolia*, Bolivia *Lewis 39497* (HO), *881131* (HO), *Bradford, Skinner and Tassin 516* (HO); *W. decora*, Madagascar *Randriamampionona 375* (HO), *Turk et al. 439* (HO); *W. ellattantha*, Peru *Diaz, Campos, Suta and Culquimboz 4584* (HO); *W. eriocarpa*, Madagascar *Turk and Solo 400* (HO); *W. fagaroides*, Ecuador *Jørgensen, Ulloa, Vargas and Abendaño 672* (HO), Bolivia, *Lewis 39419* (HO); *W. fraxinea*, Indonesia CANB109202; *W. glabra*, Costa Rica *Bello 1560* (HO); *W. humblottii*, Madagascar *Malcomber, Hutcheon, Razafimanantosa and Zjhra 1418* (HO), *Turk, Solo and Randrianasolo 319* (HO); *W. intermedia*, Mexico MIN125335, MIN125334; *W. microphylla*, Bolivia *Bradford, Bradford, Skinner and Tassin 521* (HO); *W. minutifolia*, Madagascar *Turk, Randriamanatena and Kotozafy 391* (HO); **W. parviflora*, Indonesia ANH 389324, Philippines MIN620391, Tahiti HO94953, *Hoogland and Florence 12916* (HO); *W. paulliniifolia*, Brazil CANB 00477849; *W. pentaphylla*, South America 00477853; *W. pinnata*, Costa Rica *Rivera 163* (HO), Honduras *Renfrow, Renfrow and Gunn 144* (HO), *D'Arcy 17955* (HO); *W. pullei*,

Papua New Guinea 202928; *W. pubescens*, Ecuador *Rubio and Alvarez 9621* (HO); **W. racemosa*, New Zealand HO316333, HO329959, HO81987, HO56554, MIN270761, MIN617263, MIN571188, MIN715810; *W. richii*, Fiji *Hopkins and Bradford 5025* (HO); *W. rollotii*, Ecuador *Tipaz and Quelal 1018* (HO); *W. rutenbergii*, Madagascar *Turk, Randrianasolo and Solo 220* (HO), *Schatz, Stevens and Lowry 3514* (HO); *W. sorbifolia*, Bolivia MIN125339, *Lewis 882018* (HO), *Bradford, Skinner and Tassin 511* (HO), Peru *Diaz 2118* (HO); **W. sylvicola*, New Zealand HO444307, HO316334, HO31936, MIN617172; **W. tomentosa*, Colombia Barnes collection; *W. trichophora*, Papua New Guinea ANH00476838; **W. trichosperma*, Chile CANB381113, CANB not databased, Barnes collection, HO50415; *W. turkheimii*, Honduras MIN426249; *W. urdanetensis*, Papua New Guinea CBG8315634; *W. wercklei*, Costa Rica *Aguilar 1114* (HO), *Espinoza 297* (HO).

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